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## DIATOMS OF THE INDIAN RIVER LAGOON, FLORIDA: AN ANNOTATED ACCOUNT

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**ABSTRACT:** *The Indian River Lagoon, Florida has been touted as the most diverse estuary in North America, yet the biodiversity of most biota is virtually unknown. Diatoms are abundant microalgae in this estuary, in planktonic, benthic, and epiphytic habitats. This account utilizes published records supplemented with personal observations to provide the first comprehensive summary of the diatom flora in this unusual estuary system. Apart from novel and cryptic species, 436 taxa are recorded, in 129 genera. The most diverse benthic genera were Mastogloia (36 taxa) and Nitzschia (24 taxa). Among planktonic genera were 38 taxa in Chaetoceros and 19 taxa in Thalassiosira. Sixty-two genera were represented by one species.*

**Key Words:** Indian River Lagoon, diatom, microalgae, flora

THE Indian River Lagoon (IRL) is an elongate subtropical body of water, formed within a barrier island complex, and extending for approximately one-third the length of Florida's east coast. Its exact length varies according to the varying definitions of its geographic limit: the range is 193km to 250km (120mi-155mi). Most commonly, the northern limit is considered to be the Ponce de Leon Inlet at New Smyrna Beach (29° 04.5'N, 80° 55'W), and the southern limit is the Jupiter Inlet in Palm Beach County (26° 56.5'N, 80° 04.2'W). These inlets, plus the Sebastian, Ft. Pierce and St. Lucie inlets, provide the only continuous exchange with the adjacent Atlantic Ocean. The major portions of the IRL are the Mosquito Lagoon, Banana River Lagoon, and the Indian River (including the St. Lucie River). The temperature and salinity structure throughout the length of the lagoon is highly variable on various time scales (e.g., Liu and co-workers, 1998; Niedoroda and co-workers, 1995; Smith, 1987, 1993; Virnstein, 1990). Water temperatures vary from 5–35C and salinities range from 0–38 ppt. The transitional climatic zone coupled with high variability in physical-chemical characteristics of the water masses that make up the lagoon allow for a diverse (yet poorly characterized) biota.

This region of Florida represents a significant biogeographic transition zone for both plants and animals, marine and terrestrial (Myers and Ewel, 1990;

Richards, 1995). Biota in the northern portion is more characteristic of the temperate zone (Carolinian province), while the biota of the southern portion have many features and constituents of the sub-tropical and tropical zone (Caribbean province). Recent developmental pressures have been great in the IRL (De Freese, 1995; Larson, 1995) and will likely continue so into the foreseeable future. In addition, the multiple stressors associated with consequences of anthropogenically driven global change (rising sea level, warming, invasive species, etc.) may add to the adaptive demands on IRL biota in future (De Freese, 1991). The IRL has frequently been called the most diverse estuary in North America (e.g., Hart, 1993; Adams, 1995; Herman, 1998). While this may eventually prove to be true, at present it is a specious appellation. Biodiversity is well known only for a very few groups of organisms, leaving most groups in states of partial or complete ignorance. The most recent summary of IRL biodiversity is found in Richards (1995).

Primary productivity in the IRL is a joint function of the seagrasses, marsh plants, and microalgae. Studies are sparse, but seagrass and marsh productivity appears typical for warm temperate areas (Myers and Ewel, 1990; Dawes and co-workers, 1995). Substantial spatial and temporal variability in productivity is a feature of the IRL (Heffernan and Gibson, 1984). In one study, over 70% of the primary productivity was shown to be due to planktonic microalgae (Jensen and Gibson, 1986), with a 5% contribution by benthic microalgae. The diatoms of this lagoon system are presumably one of the main contributors to microalgal primary productivity, by virtue of their abundance and ubiquity, but comprehensive productivity studies are lacking. Moreover, the contribution to primary productivity by phototrophic and mixotrophic microflagellates (which are often abundant; pers. obs.) is unknown. Plankton chlorophyll ranges exceed two orders of magnitude throughout the lagoon, ( $<0.1$  to  $>20$   $\mu\text{g/l}$ : Youngbluth and co-workers, 1976; Mahoney and Gibson, 1983b; and pers. obs.) of which 40–70% may be diatoms, yet their diversity has been examined only sporadically and incompletely over the last several decades. This is surprising, given the local, regional, and national economic importance and biological significance of the IRL. Several unpublished theses, some preliminary surveys, and studies restricted to single or a few genera constitute most of the available literature. There are also parts of the IRL, such as the Banana River and St Lucie River system, which have never been examined in any detail. Nevertheless, the number of recorded diatom taxa from the IRL is substantial. A series of seasonal samples collected in 1997–2001, an extended sampling series in winter 2000, and an extensive literature search resulted in a significant expansion of the diatom flora from the earlier list of Mahoney and Gibson (1983a).

**METHODS—Sample collection**—In each season of 1998, 1999, and 2000, and winter/spring of 2001 plankton samples were collected with a 20 $\mu\text{m}$  mesh net in the IRL at Vero Beach and at the Sebastian and Ft Pierce inlets; IRL sediment surface samples at Memorial Park, Vero Beach, and at Ft Pierce inlet; and seagrass (*Halodule* and *Syringodium*), *Rhizophora mangle* and *Spartina* samples (for epiphytes) in the IRL at Oslo Rd. and Memorial Park, Vero Beach. During winter 2000, similar plankton, sediment, and epiphyte samples were collected in the IRL at Eau Gallie Causeway, St Sebastian River, Sebastian Inlet, Vero Beach at Memorial Park and Oslo Rd., ship channel at Harbor Branch Oceanographic Institute, Ft Pierce Inlet, Stuart Causeway, and St Lucie Inlet.

*Sample processing*—Aliquots of preserved samples were washed free of salt with sequential centrifugation and dilution with deionized water. For light microscopy, samples were processed in two ways: duplicate sub-aliquots were evaporated on hot plates, then heated to oxidize all organic material, then mounted in a high refractive index mounting medium (Hyrax or Naphrax); other duplicate sub-aliquots were boiled for 1hr in 30% hydrogen peroxide, sequentially centrifuged and washed in deionized water, and mounted in Hyrax or Naphrax. For scanning and transmission electron microscopy, preparation was similar, except sub-aliquots were mounted on copper boats (SEM) or formvar/carbon coated grids (TEM) and coated with Au/Pt or carbon (SEM only).

*Sample analysis*—For light microscopy, a Zeiss Photomicroscope-II or Nikon LKe with bright-field, phase contrast and interference contrast were used; for electron microscopy, a Zeiss EM9S (TEM), and (for SEM) JEOL 1200EX or JSM6400 were used.

*Literature*—Few published papers give details on the IRL diatom flora. Several that were used in compiling this list are: Stephens and Gibson (1976, 1979); Tester and Steidinger (1979); Navarro (1982); Mahoney and Gibson (1983a); and Lu (1987). There are pitfalls in accepting such published lists at face value. The skill levels in accurate identification vary among authors, particularly when availability of pertinent monographs is uncertain. Spelling and orthographic errors, and changes in taxon limits and nomenclature all lead to disjuncts and inconsistencies in compiling accurate records. Some of these published records cite species authorities, others do not. I have dealt with these problems by accepting the identifications as stated, but making nomenclatural changes as necessary and including species authorities, deleting species only when egregious mistakes are suspected (e.g., an Antarctic species recorded from the IRL in mid-summer). For common or abundant taxa, synonymous names are included when the previously published name differs from the currently accepted name. Strictly speaking the Tester and Steidinger (1979) paper includes diatom occurrences outside the IRL (about 10km S of the Ft Pierce Inlet), but I have found nearly all their included species through tidal cycles at the Ft. Pierce inlet, so have included their records.

*Taxonomic scheme*—Diatom taxonomy is in a state of controversy and ferment: opinions on grouping of species into genera, genera to families, etc. are changing constantly. In general this uncertainty and controversy is avoided by listing taxa alphabetically within defined orders without separation into families, and by briefly comparing the contrasting ordinal scheme as delimited in Round and co-workers (1990) vs. that of Hasle and Syvertsen (1997). This is not a wholly satisfactory arrangement, since an unjustified relationship may be implied, but avoids making decisions that may prove untenable in future. Accordingly, the diatoms are grouped in five orders.

**RESULTS**—Four hundred thirty-six diatom taxa in 129 genera are designated as present in the IRL. A number of species require explanatory notes, and these are ordered below. In the annotated list, presented as an appendix, the habitus and distribution are briefly indicated for each taxon as two letter codes, as gleaned from other global records.

*Habitus:*

B = primarily benthic, including epipelagic, epilithic, and epipsammic microhabitats;

E = primarily epiphytic on seaweeds and marine higher plants (or, for *Proto-rhaphis* and *Pseudohimantidium*, epizoic);

P = primarily planktonic in dominant life form (resting spores may be benthic)

*Distribution:*

T = primarily a warm-water or tropical taxon;

C = primarily a warm or cold temperate taxon;

W = widespread or cosmopolitan in temperate and tropical waters;  
F = primarily confined to oligohaline (<5 ppt) or fresh water.

DISCUSSION—The reported presence of 436 diatoms from the IRL seems remarkable, but in reality this number does not represent the entire diversity. Although a substantial portion of the planktonic taxa has probably been identified, many of the benthic forms are almost certainly underrepresented. In part this is a result of incomplete and sporadic sampling. The majority of published works on diatoms in the IRL have been based on samples collected at or near the Harbor Branch Oceanographic Institute in Ft. Pierce (e.g., Mahoney and Gibson, 1983a; Navarro, 1982). Likewise, many of the additional new records recorded by me were ancillary to other experiments undertaken in the same general area. The result is that regions of the IRL with major hydrographic and ecological differences from the central IRL have yet to be examined. The Mosquito Lagoon, for example, is clearly differentiated from adjacent areas on the basis of fish and invertebrate biodiversity (Paperno and co-workers, 2001) and the microalgal community surely has unique features as well. Likewise, to the south, the St Lucie River, with its eutrophication stress is likely to harbor species amenable to nutrient-rich areas that are not found farther north. Certainly the chlorophyll levels here (up to 120µg/liter; Doering 1996) indicate a substantial microalgal population whose constituents are unknown. Moreover, there are several novel species from the plankton not included in his account, yet to be described formally. Close examination of diatom communities elsewhere in Florida also has resulted in the discovery of new species (Prasad and co-workers, 1989; 2000): an expected result when the communities are examined in depth.

Several diatom taxa are potentially harmful to humans or marine life. All the *Pseudo-nitzschia* species reported from the IRL (*P. delicatissima*, *P. pseudodelicatissima*, *P. pungens*, *P. seriata*) have been reported to produce domoic acid under some circumstances elsewhere (Hargraves and Maranda, 2002). Domoic acid is a neurotoxin, the cause of amnesic shellfish poisoning (ASP), so far unknown from the east coast of Florida (for domoic acid and *Pseudo-nitzschia* references, see Bates, 2002 or NIEHS, 2002). Domoic acid was responsible for human poisoning events on the Atlantic coast of Canada and the northwest coast of the U.S. At present it is unknown whether IRL strains of these species produce domoic acid, but in most areas these species appear to be benign.

Some of these diatoms are known to produce excreted metabolites that interfere with normal functioning or life cycle events in marine animals. These include *Coscinodiscus centralis*, *Coscinodiscus wailesii*, *Cerataulina pelagica*, and *Chaetoceros debilis* (Hargraves and Maranda, 2002). Others, such as the epizoic diatoms *Protoraphis atlantica* and *Pseudohimantidium pacificum*, mechanically reduce the motility of their hosts, thus interfering with reproduction and perhaps increasing their vulnerability to predators.

There are likely invasive species of diatoms in the IRL, although insufficient prior records make an accurate assessment speculative. The intense rates of transit

by recreational and commercial boats, with ballast water discharge and fouling communities, as well as migratory waterfowl, with residual attached biota, provide ample vectors for the introduction of nonindigenous species. Their eventual survival and success is less certain, however, and depends on a number of interacting parameters (Carlton and Geller, 1993; Carlton, 1996). *Coscinodiscus wailesii* is surely an invasive species in the IRL, having appeared on the U.S. east coast in the late 1970's. Many others may be termed "cryptogenic": they may be recent introductions, but there is insufficient background information to confirm this at present. Examples of cryptogenic species include *Thalassiosira proschkinae*, previously known from European coastal waters and recently discovered in Narragansett Bay, Rhode Island (pers. obs.), and *Minidiscus comicus*, a tiny species that is apparently widespread but mostly overlooked because of its size (2–5  $\mu\text{m}$ ).

The IRL faces increasing anthropogenic pressure, on local, regional and global scales. Recent management initiatives have focused attention on more visually obvious members of the ecosystem: manatees, fish, seagrasses, etc. The stressors for these biota are not always the same as stressors for the microalgae, which form the base of the food web. In order to evaluate the efficacy of management plans for the entire ecosystem, biodiversity at all trophic levels must be examined. The more difficult task for the future is separating local and regional anthropogenic influences on biodiversity, from those associated with broader global climate change.

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## APPENDIX

Diatoms from the Indian River Lagoon. See text for notes and abbreviations

### COSCONODISCALES

As considered here, the characteristics defining this order are: valve symmetry primarily with no polarities (i.e., oriented around a point rather than a line), and mostly with a marginal ring of various structural processes. In the taxonomic scheme proposed by Round, Crawford and Mann (1990), the species included

here in the Coscinodiscales encompass four different orders. In the scheme followed by Hasle and Syvertsen (1997), this order corresponds to their suborder Coscinodiscineae.

<i>Actinocyclus normanii</i> (Gregory) Hustedt	(P, W)
<i>Actinocyclus octonarius</i> Ehrenberg	(P, W)
<i>Actinocyclus octonarius</i> var. <i>crassus</i> (W. Smith) Hendey	(P, C)
<i>Actinocyclus octonarius</i> var. <i>tenellus</i> (Brébisson) Hendey	(P, C)
<i>Actinoptychus senarius</i> Ehrenberg	(B, W)
<i>Actinoptychus splendens</i> (Shadbolt) Ralfs	(B, W)
<i>Aulacodiscus argus</i> (Ehrenberg) A. Schmidt	(B, W)
<i>Aulacoseira islandica</i> (O. Müller) Simonsen	(P, F)
synonym: <i>Melosira islandica</i> O. Müller	
<i>Corethron hystrix</i> Cleve	(P, W)
<i>Coscinodiscus centralis</i> Ehrenberg	(P, W)
<i>Coscinodiscus granii</i> Gough	(P, W)
<i>Coscinodiscus oculus-iridis</i> Ehrenberg	(P, W)
<i>Coscinodiscus perforatus</i> Ehrenberg	(P, W)
<i>Coscinodiscus radiatus</i> Ehrenberg emend. Hasle et Sims	(P, W)
<i>Coscinodiscus walesii</i> Gran et Angst	(P, C)
<i>Cyclotella atomus</i> Hustedt	(P, C)
<i>Cyclotella choctawhatcheeana</i> Prasad	(P, W)
<i>Cyclotella meneghiniana</i> Kützing	(B, W)
<i>Cyclotella stelligera</i> Cleve et Grunow	(B, F)
<i>Cyclotella striata</i> (Kützing) Grunow	(P, W) [note 1]
<i>Cyclotella stylorum</i> Brightwell	(P, T)
<i>Detonula pumila</i> (Castracane) Schütt	(P, W)
synonym: <i>Schroederella delicatula</i> Pavillard	
<i>Hyalodiscus scoticus</i> (Kützing) Grunow	(E, C)
<i>Hyalodiscus subtilis</i> Bailey	(E, C)
<i>Lauderia annulata</i> Cleve	(P, C)
synonym: <i>Lauderia borealis</i> Gran	
<i>Leptocylindrus danicus</i> Cleve	(P, C)
<i>Leptocylindrus minimus</i> Gran	(P, C)
<i>Melosira lineata</i> (Dillwyn) Agardh	(E, C)
synonym: <i>M. juergensii</i> Agardh	
<i>Melosira moniliformis</i> (O. Müller) Agardh	(E, C)
<i>Melosira nummuloides</i> (Dillwyn) Agardh	(E, C)
<i>Minidiscus comicus</i> Takano	(P, W)
<i>Palmeria hardmanniana</i> Greville	(P, T)
<i>Paralia sulcata</i> (Ehrenberg) Cleve	(P, W)
<i>Planktoniella sol</i> (Wallich) Schütt	(P, W)
<i>Podosira hormoides</i> (Montagne) Kützing	(E, T)
<i>Podosira montagnei</i> Kützing	(E, T)
<i>Podosira stelliger</i> (Bailey) A. Mann	(E, T) [note 2]

<i>Skeletonema costatum</i> (Greville) Cleve	(P, W)
<i>Skeletonema menzeli</i> Guillard, Carpenter et Reimann	(P, C)
<i>Skeletonema tropicum</i> Cleve	(P, T)
<i>Stephanopyxis palmeriana</i> (Greville) Grunow	(P, C)
<i>Stephanopyxis turris</i> (Greville et Arnott) Ralfs	(P, W)
<i>Thalassiosira aestivalis</i> Gran	(P, C)
<i>Thalassiosira anguste-lineata</i> (Schmidt) Fryxell	(P, W)
<i>Thalassiosira binata</i> Fryxell	(P, C)
<i>Thalassiosira decipiens</i> (Grunow) Jörgensen	(B, W) [note 3]
<i>Thalassiosira diporocyclus</i> Hasle	(P, W)
<i>Thalassiosira eccentrica</i> (Ehrenberg) Cleve	(P, W)
synonym: <i>Coscinodiscus eccentricus</i> Ehrenberg	
<i>Thalassiosira exigua</i> Fryxell et Hasle	(P, W)
<i>Thalassiosira gravida</i> Cleve	(P, C)
<i>Thalassiosira hyalina</i> (Grunow) Gran	(P, C)
<i>Thalassiosira lineata</i> Jousé	(P, T)
<i>Thalassiosira lundiana</i> Fryxell	(P, C)
<i>Thalassiosira minima</i> Gaarder emend. Hasle	(P, W)
synonym: <i>T. floridana</i> (Cooper) Hasle	
<i>Thalassiosira minuscula</i> Krasske	(P, C)
<i>Thalassiosira nanolineata</i> (Mann) Fryxell et Hasle	(P, T)
<i>Thalassiosira oestrupii</i> (Ostenfeld) Proschkina-Lavrenko	
var. <i>venrickae</i> Fryxell et Hasle	(P, W)
<i>Thalassiosira proschkinae</i> Makarova	(P, W)
<i>Thalassiosira rotula</i> Meunier	(P, W) [note 4]
<i>Thalassiosira subtilis</i> (Ostenfeld) Gran	(P, C)
<i>Thalassiosira weissflogii</i> (Grunow) Fryxell et Hasle	(P, F)
synonym: <i>T. fluviatilis</i> Hustedt	

## RHIZOLENIALES

As considered here, the characteristics defining this order are: valves symmetry organized around a point or annulus, primarily unipolar, and lacking a ring of various structural processes. In the taxonomic scheme proposed by Round and co-workers (1990), the species included here in the Rhizosoleniales encompass two different orders. In the scheme followed by Hasle and Syvertsen (1997), this order corresponds to their families Rhizosoleniaceae and Lithodesmiaceae.

<i>Dactyliosolen fragilissimus</i> (Bergon) Hasle	(P, W)
synonym: <i>Rhizosolenia fragilissima</i> Bergon	
<i>Guinardia delicatula</i> (Cleve) Hasle	(P, W)
synonym: <i>Rhizosolenia delicatula</i> Cleve	
<i>Guinardia flaccida</i> (Castracane) Peragallo	(P, W)
<i>Guinardia striata</i> (Stolterfoth) Hasle	(P, W)
synonym: <i>Rhizosolenia stolterfothii</i> Peragallo	
<i>Lithodesmium intricatum</i> (West) Peragallo	(P, C)
<i>Lithodesmium undulatum</i> Ehrenberg	(P, C)
<i>Proboscia alata</i> (Brightwell) Sundström	(P, W)
synonym: <i>Rhizosolenia alata</i> Brightwell	
<i>Proboscia indica</i> (Peragallo) Hernández-Becerril	(P, T)

synonym: *Rhizosolenia alata forma indica* (Peragallo) Ostenfeld

<i>Pseudosolenia calcar-avis</i> (Schultze) Sundström	(P, W)
<i>Rhizosolenia bergonii</i> Peragallo	(P, T)
<i>Rhizosolenia castracanei</i> Peragallo	(P, T)
<i>Rhizosolenia hebetata</i> Bailey <i>forma semispina</i> (Hensen) Gran	(P, C)
<i>Rhizosolenia imbricata</i> Brightwell	(P, W)
<i>Rhizosolenia robusta</i> Norman	(P, W) [note 5]
<i>Rhizosolenia setigera</i> Brightwell	(P, W)
<i>Rhizosolenia styliformis</i> Brightwell	(P, C)

## BIDDULPHIALES

As considered here, the characteristics defining this order are: valves symmetrically organized around a point or annulus, primarily bipolar (but sometimes multipolar), and lacking a ring of various structural processes. In the taxonomic scheme proposed by Round and co-workers (1990), the species included here in the Biddulphiales encompass eight different orders. In the scheme followed by Hasle and Syvertsen (1997), this order corresponds to the suborder Biddulphiineae.

<i>Amphitetras antediluviana</i> Ehrenberg	(E, W)
synonym: <i>Triceratium antediluvianum</i> (Ehrenberg) Grunow	
<i>Auliscus caelatus</i> Bailey <i>var. rhipis</i> (A. Schmidt) Peragallo	(B, W) [note 6]
<i>Auliscus caelatus</i> <i>var. strigillata</i> A. Schmidt	(B, W)
<i>Auliscus pruinosis</i> Bailey	(B, W) [note 7]
<i>Auliscus punctatus</i> Bailey	(B, W) [note 7]
<i>Auliscus radiatus</i> Bailey	(B, W)
<i>Auliscus reticulatus</i> Greville	(B, W)
<i>Auliscus sculptus</i> (W. Smith) Ralfs	(B, W)
<i>Bacteriastrum delicatulum</i> Cleve	(P, W)
<i>Bacteriastrum hyalinum</i> Lauder	(P, W)
<i>Bellerochea horologicalis</i> von Stosch	(P, T)
<i>Biddulphia alternans</i> (Bailey) Van Heurck	(E, W) [note 8]
<i>Biddulphia biddulphiana</i> (J. Smith) Boyer	(E, W)
synonym: <i>B. pulchella</i> Gray	
<i>Biddulphia reticulata</i> Roper	(E, W)
<i>Biddulphia tuomeyi</i> (Bailey) Roper	(E, T)
<i>Cerataulina pelagica</i> (Cleve) Hendey	(P, W)
<i>Cerataulus smithii</i> Ralfs	(B, W)
<i>Chaetoceros affinis</i> Lauder	(P, W)
<i>Chaetoceros affinis</i> <i>var. willei</i> (Gran) Hustedt	(P, W)
<i>Chaetoceros anastomosans</i> Grunow	(P, W)
<i>Chaetoceros brevis</i> Schütt	(P, W) [note 9]
<i>Chaetoceros cinctus</i> Gran	(P, W)
<i>Chaetoceros coarctatus</i> Lauder	(P, T)
<i>Chaetoceros compressus</i> Lauder	(P, W)
<i>Chaetoceros constrictus</i> Gran	(P, C)
<i>Chaetoceros curvisetus</i> Cleve	(P, W)
<i>Chaetoceros danicus</i> Cleve	(P, W)

<i>Chaetoceros debilis</i> Cleve	(P, W)
<i>Chaetoceros decipiens</i> Cleve	(P, W) [note 10]
<i>Chaetoceros diadema</i> (Ehrenberg) Gran	(P, C)
<i>Chaetoceros didymus</i> Ehrenberg	(P, W)
<i>Chaetoceros didymus</i> var. <i>anglicus</i> (Grunow) Gran	(P, W)
<i>Chaetoceros diversus</i> Cleve	(P, T)
<i>Chaetoceros eibonii</i> Grunow emend. Meunier	(P, C)
<i>Chaetoceros gracilis</i> Schütt	(P, W) [note 11]
<i>Chaetoceros lacinosus</i> Schütt	(P, C)
<i>Chaetoceros lauderi</i> Ralfs	(P, W)
<i>Chaetoceros lorenzianus</i> Grunow	(P, T) [note 10]
<i>Chaetoceros lorenzianus</i> var. <i>forceps</i> Meunier	(P, W)
<i>Chaetoceros messanensis</i> Castracane	(P, T)
<i>Chaetoceros minimus</i> (Levander) Marini, Giuffre, Montessor et Zingone	(P, F)
<i>Chaetoceros muelleri</i> Lemmerman	(P, F)
<i>Chaetoceros neogracilis</i> Van Landingham	(P, W) [note 11, 12]
<i>Chaetoceros pelagicus</i> Cleve	(P, C)
<i>Chaetoceros pendulus</i> Karsten	(P, T) [note 13]
<i>Chaetoceros peruvianus</i> Brightwell	(P, W) [note 13]
<i>Chaetoceros protuberans</i> Lauder	(P, W)
<i>Chaetoceros pseudocurvisetus</i> Mangin	(P, T)
<i>Chaetoceros simplex</i> Ostenfeld	(P, W) [note 11]
<i>Chaetoceros socialis</i> Lauder	(P, C)
<i>Chaetoceros subtilis</i> Cleve	(P, F)
<i>Chaetoceros teres</i> Cleve	(P, C)
<i>Chaetoceros tortissimus</i> Gran	(P, W)
<i>Chaetoceros vistulae</i> Apstein	(P, F)
<i>Chaetoceros wighami</i> Brightwell	(P, F)
<i>Climacodium frauenfeldianum</i> Grunow	(P, T)
<i>Cymatosira belgica</i> Grunow	(B, C)
<i>Cymatosira lorenziana</i> Grunow	(B, W)
<i>Ditylum brightwellii</i> (West) Grunow	(P, W)
<i>Eucampia cornuta</i> (Cleve) Grunow	(P, T)
<i>Eucampia zodiacus</i> Ehrenberg	(P, W)
<i>Eunotogramma laevis</i> Grunow	(B, W)
<i>Eunotogramma marinum</i> (W. Smith) Peragallo	(B, W)
<i>Eunotogramma rostratum</i> Hustedt	(B, C)
<i>Eupodiscus radiatus</i> Bailey	(B, W) [note 14]
<i>Helicotheca tamesis</i> (Shrubsole) Ricard	(P, W)
<i>Hemiaulus hauckii</i> Grunow	(P, W)
<i>Hemiaulus membranaceus</i> Cleve	(P, T)
<i>Hemiaulus sinensis</i> Greville	(P, W)
synonym: <i>H. heibergii</i> Cleve	
<i>Isthmia enervis</i> Ehrenberg	(E, T)
<i>Lampriscus shadboltianus</i> (Greville) Peragallo	(E, T) [note 15]
synonym: <i>Triceratium shadboltianum</i> Greville	
<i>Lithodesmium undulatum</i> Ehrenberg	(P, C)

<i>Minutocellus polymorphus</i> (Hargraves et Guillard) Hasle, v. Stosch et Syvertsen	(P, W)
<i>Odontella aurita</i> Agardh	(E, W)
<i>Odontella aurita</i> var. <i>minuscula</i> Grunow	(E, W)
<i>Odontella aurita</i> var. <i>obtusa</i> (Kützing) Hustedt	(E, W)
<i>Odontella longicruris</i> (Greville) Hoban	(P, W)
<i>Odontella mobiliensis</i> Grunow	(P, W)
<i>Odontella regia</i> (Schultze) Hoban	(P, W)
<i>Odontella rhombus</i> (Ehrenberg) Kützing	(P, W)
<i>Odontella sinensis</i> (Greville) Grunow	(P, W)
<i>Pleurosira laevis</i> (Ehrenberg) Compère	(E, T)
<i>Terpsinoë americana</i> (Bailey) Ralfs	(E, F)
<i>Terpsinoë musica</i> Ehrenberg	(E, F)
<i>Triceratium antediluvianum</i> (Ehrenberg) Grunow	(B, C) [note 16]
<i>Triceratium balearicum</i> Cleve forma <i>biquadrata</i> (Janisch) Hustedt synonym: <i>T. biquadratum</i> Janisch	(B, C) [note 16, 17]
<i>Triceratium dubium</i> Brightwell	(B, C)
<i>Triceratium favus</i> Ehrenberg	(B, W)
<i>Triceratium favus</i> var. <i>quadrata</i> Grunow	(B, W)
<i>Triceratium pentacrinus</i> (Ehrenberg) Wallich	(B, W) [note 16, 17, 18]
<i>Triceratium pentacrinus</i> forma <i>quadrata</i> Hustedt	(B, W)
<i>Trigonium reticulum</i> (Ehrenberg) Simonsen	(E, W) [note 16, 19]

## FRAGILARIALES

As considered here, the characteristics defining this order are: bilaterally symmetrical valves, lacking a raphe on either valve, but often with a hyaline sternum (equivalent to the pseudoraphe or axial area of other texts). The areolae are arranged more or less linear fashion in relation to the sternum. The species contained here encompass nine orders in Round and co-workers (1990). This order is subsumed in Bacillariales in the scheme adopted by Hasle and Syvertsen (1997).

<i>Ardissonea fulgens</i> (Greville) Grunow	(E, W) [note 20, 21]
<i>Ardissonea pulcherrima</i> (Hantzsch) Grunow	(E, T)
<i>Ardissonea robusta</i> (Ralfs) DeNotaris	(E, W)
<i>Asterionellopsis glacialis</i> (Castracane) Round	(P, W)
<i>Bleakeleya notata</i> (Grunow) Round	(P, T)
<i>Catacombas gaillonii</i> (Bory) Williams et Round	(E, W) [note 20]
<i>Climacosphenia elongata</i> Bailey	(E, T)
<i>Delphineis surirella</i> (Ehrenberg) Andrews	(B, W)
<i>Delphineis surirella</i> var. <i>australis</i> (Petit) Navarro	(B, T)
<i>Dimeregramma minor</i> (Gregory) Ralfs	(B, W)
<i>Dimeregramma minor</i> var. <i>nana</i> (Gregory) Van Heurck	(B, W)
<i>Falcula media</i> Voigt	(E, W) [note 22]
<i>Fragilaria capucina</i> Desmazières var. <i>mesolepta</i> Rabenhorst	(P, F)
<i>Fragilaria virescens</i> Ralfs var. <i>mesolepta</i> Rabenhorst	(P, F)

<i>Glyphodesmis williamsonii</i> (W. Smith) Grunow	(B, T)
<i>Grammatophora gibberula</i> Kützing	(E, C)
<i>Grammatophora marina</i> (Lyngbye) Kützing	(E, W)
<i>Grammatophora marina</i> var. <i>tropica</i> (Kützing) Grunow	(E, T)
<i>Grammatophora oceanica</i> (Ehrenberg) Grunow	(E, W)
<i>Grammatophora oceanica</i> var. <i>macilenta</i> (W. Smith) Grunow	(E, W)
<i>Grammatophora serpentina</i> (Ralfs) Ehrenberg	(E, W)
<i>Hyalosynedra laevigata</i> (Grunow) Williams et Round	(E, T) [note 23]
<i>Hyalosira interrupta</i> (Ehrenberg) Navarro	(E, T) [note 24]
synonym: <i>Striatella interrupta</i> (Ehrenberg) Heiberg	
<i>Licmophora abbreviata</i> Agardh	(E, W)
<i>Licmophora abbreviata</i> forma <i>grunowii</i> (Mereschkowsky) Hustedt	(E, W)
<i>Licmophora ehrenbergii</i> (Kützing) Grunow	(E, C)
<i>Licmophora flabellata</i> (Carmichael) Agardh	(E, W)
<i>Licmophora paradoxa</i> (Lyngbye) Agardh	(E, W)
<i>Licmophora remulus</i> Grunow	(E, T)
<i>Lioloma pacificum</i> (Cupp) Hasle	(P, C)
<i>Martyana martyi</i> (Héribaud) Round	(B, F)
synonym: <i>Opephora martyi</i> Héribaud	
<i>Nanofrustulum shiloi</i> (Lee, Reimer et McEnery) Round, Hallsteinsen et Paasche	(P, W) [note 37]
<i>Opephora marina</i> (Gregory) Petit	(B, W)
<i>Opephora mutabilis</i> (Grunow) Sabbe et Vyverman	(B, W) [note 25]
synonym: <i>Opephora olsenii</i> Möller	
<i>Opephora pacifica</i> (Grunow) Petit	(B, W)
<i>Opephora schwartzii</i> (Grunow) Petit	(B, C)
<i>Plagiogramma interruptum</i> (Gregory) Ralfs	(B, T)
<i>Plagiogramma pulchellum</i> Greville var. <i>pygmaea</i> (Greville) Peragallo	(B, T)
synonym: <i>Plagiogramma pygmaeum</i> Greville	
<i>Plagiogramma rhombicum</i> Hustedt	(B, C)
<i>Plagiogrammopsis vanheurckii</i> (Grunow) Hasle, v. Stosch et Syvertsen	(B, W)
<i>Plagiogrammopsis wallichianum</i> Greville	(B, C)
<i>Podocystis adriatica</i> Kützing	(E, C)
<i>Protoraphis atlantica</i> Gibson	(E, P)
<i>Psammodiscus nitidus</i> (Gregory) Round et Mann	(B, W)
synonym: <i>Coscinodiscus nitidus</i> Gregory	
<i>Pseudohimantidium pacificum</i> Hustedt et Krasske	(E, P)
<i>Pteroncola inane</i> (Giffen) Round	(E, W) [note 26]
synonym: <i>Fragilaria hyalina</i> (Kützing) Grunow	
<i>Rhabdonema adriaticum</i> Kützing	(E, W)
<i>Rhabdonema arcuatum</i> (Lyngbye) Kützing	(E, W)

<i>Rhaphoneis amphiceros</i> Ehrenberg	(B, W)
<i>Rhaphoneis amphiceros</i> var. <i>gemmifera</i> (Ehrenberg) Peragallo	(B, W)
<i>Rhaphoneis castracanei</i> Grunow	(B, T)
<i>Rhaphoneis superba</i> Grunow	(B, T)
<i>Striatella unipunctata</i> (Lyngbye) Agardh	(E, C)
<i>Tabularia fasciculata</i> (Agardh) Williams et Round	(E, W)
synonym: <i>Synedra tabulata</i> (Agardh) Kützing	
var. <i>fasciculata</i> (Agardh) Hustedt	
<i>Tabularia parva</i> (Kützing) Williams et Round	(E, W)
synonym: <i>S. tabulata</i> var. <i>parva</i> (Kützing) Hustedt	
<i>Tabularia tabulata</i> (Agardh) Snoeijis	(E, W)
synonym: <i>Synedra tabulata</i> (Agardh) Kützing	
<i>Thalassionema frauenfeldii</i> (Grunow) Hallegraeff	(P, W)
<i>Thalassionema nitzschioides</i> (Grunow) Mereschkowsky	(P, W)
<i>Toxarium hennedyanum</i> Grunow	(E, C) [note 27]
<i>Trachysphenia acuminata</i> Peragallo	(B, C)

## BACILLARIALES

As considered here, the characteristics defining this order are: bilaterally symmetrical valves, and the presence of a raphe on one or both valves. In the taxonomic scheme proposed by Round and co-workers (1990), the species included here in the Bacillariales encompass nine different orders. The order Bacillariales in the sense of Hasle and Syvertsen (1997) would include the order Fragilariales as considered in this work.

<i>Achnanthes brevipes</i> Agardh	(E, C)
<i>Achnanthes brevipes</i> var. <i>angustata</i> (Greville) Cleve	(E, C)
<i>Achnanthes brevipes</i> var. <i>parvula</i> (Kützing) Cleve	(E, C)
<i>Achnanthes citronella</i> (Mann) Hustedt	(E, C)
<i>Achnanthes curvirostrum</i> Brun	(E, C)
<i>Achnanthes kuwaitensis</i> Hendey	(E, T)
<i>Achnanthes longipes</i> Agardh	(E, W)
<i>Achnanthes manifera</i> Brun	(E, C)
<i>Amphora angusta</i> Gregory	(B, F)
<i>Amphora angusta</i> var. <i>ventricosa</i> (Gregory) Cleve	(B, F)
<i>Amphora arenaria</i> Donkin	(B, F)
<i>Amphora bigibba</i> Grunow	(B, T)
<i>Amphora caroliniana</i> Giffen	(B, C)
<i>Amphora coffaeiformis</i> Agardh	(B, W) [note 28]
<i>Amphora costata</i> W. Smith	(B, W)
<i>Amphora decussata</i> Grunow	(B, T)
<i>Amphora exigua</i> Gregory	(B, W)
<i>Amphora marina</i> (W. Smith) Van Heurck	(B, C)
<i>Amphora obtusa</i> Gregory	(B, C)
<i>Amphora ocellata</i> Donkin	(B, C)
<i>Amphora ostrearia</i> Brébisson var. <i>lineata</i> Cleve	(B, C)
<i>Amphora proteoides</i> Hustedt	(B, C)
<i>Amphora proteus</i> Gregory	(B, C)

<i>Amphora robusta</i> Gregory	(B, C)
<i>Amphora spectabilis</i> Gregory	(B, C)
<i>Amphora terroris</i> Ehrenberg	(B, T)
synonym: <i>A. cymbifera</i> Gregory	
<i>Anomoeoneis sphaerophora</i> (Kützing) Pfitzer var. <i>sculpta</i> (Ehrenberg) O. Möller	(B, F)
<i>Anorthoneis eurystoma</i> Cleve	(B, T)
<i>Anorthoneis excentrica</i> (Donkin) Grunow	(B, C)
<i>Anorthoneis hyalina</i> Hustedt	(B, C)
<i>Auricula complexa</i> (Gregory) Cleve	(B, C)
<i>Bacillaria paxillifer</i> (O. Müller) Hendey	(B, W) [note 29]
<i>Berkeleya micans</i> (Lyngbye) Gran	(B, C) [note 30]
<i>Berkeleya rutilans</i> (Trentepohl) Grunow	(B, C) [note 30]
<i>Caloneis elongata</i> (Grunow) Boyer	(B, F) [note 31]
<i>Caloneis excentrica</i> (Grunow) Boyer	(B, F) [note 31]
<i>Campylodiscus daemelianus</i> Grunow	(B, T)
<i>Campylodiscus innominatus</i> Ross et Abdin	(B, C)
<i>Capartogramma crucicula</i> (Grunow) Ross	(B, C)
<i>Climaconeis lorenzii</i> Grunow	(B, T) [note 32]
<i>Cocconeis brittanica</i> Naegeli	(E, W)
<i>Cocconeis convexa</i> Giffen	(E, C)
<i>Cocconeis disculooides</i> Hustedt	(E, C)
<i>Cocconeis heteroidea</i> Hantsch	(E, T)
<i>Cocconeis pellucida</i> Grunow	(E, W)
<i>Cocconeis placentula</i> Ehrenberg	(E, F)
<i>Cocconeis placentula</i> var. <i>euglypta</i> (Ehrenberg) Cleve	(E, F)
<i>Cocconeis pseudomarginata</i> Gregory	(E, C)
<i>Cocconeis scutellum</i> Ehrenberg	(E, W)
<i>Cocconeis scutellum</i> var. <i>stauroneiformis</i> W. Smith	(E, W)
<i>Cocconeis woodii</i> Reyes-Vasquez	(E, T)
<i>Cylindrotheca closterium</i> (Ehrenberg) Reimann et Lewin	(B, W)
<i>Cymbella pusilla</i> Grunow	(B, F)
<i>Denticula subtilis</i> Grunow	(B, F)
<i>Denticula thermalis</i> Kützing	(B, F)
<i>Diadesmis contenta</i> (Grunow) Mann	(B, F)
synonym: <i>Navicula contenta</i> Grunow	
<i>Dictyoneis marginata</i> (Lewis) Cleve	(B, T)
<i>Diploneis bombus</i> Ehrenberg	(B, W)
<i>Diploneis crabro</i> Ehrenberg	(B, W)
<i>Diploneis gravelleana</i> Hagelstein	(B, T)
<i>Diploneis gruendleri</i> (Schmidt) Cleve	(B, C)
<i>Diploneis interrupta</i> (Kützing) Cleve var. <i>caffra</i> Giffen	(B, C)
<i>Diploneis obliqua</i> (Brun) Hustedt	(B, C)

- Diploneis smithii* (Brèbisson) Cleve (B, W)  
*Diploneis suborbicularis* (Gregory) Cleve var. *constricta* Hustedt (B, C)  
*Diploneis vacillans* (Schmidt) Cleve var. *renitens* Schmidt (B, T)  
*Diploneis weissflogii* (Schmidt) Cleve (B, W)  
  
*Entomoneis alata* (Ehrenberg) Ehrenberg (B, W)  
*Entomoneis pulchra* (Bailey) Reimer (B, T)  
 synonym: *Amphiprora conspicua* Greville  
  
*Epithemia sorex* Kützing (B, F)  
  
*Fallacia amphipleuroides* (Hustedt) Mann (B, C) [note 33]  
*Fallacia forcipata* (Greville) Stickle et Mann (B, C)  
*Fallacia hyalinula* (DeToni) Stickle et Mann (B, C)  
*Fallacia litoricola* (Hustedt) Mann (B, C)  
*Fallacia nummularia* (Greville) Mann (B, C)  
  
*Frustulia asymmetrica* (Cleve) Hustedt (B, T)  
  
*Gomphonema acuminatum* Ehrenberg (E, F)  
  
*Gomphonemopsis littoralis* (Hendey) Medlin (E, T)  
  
*Gyrosigma baileyi* (Grunow) Cleve (B, C)  
*Gyrosigma balticum* (Ehrenberg) Rabenhorst (B, W)  
*Gyrosigma fasciola* (Ehrenberg) Griffith et Henfrey (B, W)  
*Gyrosigma hummii* Hustedt (B, C)  
*Gyrosigma macrum* (W. Smith) Griffith et Henfrey (B, C)  
*Gyrosigma peisonis* (Grunow) Hustedt (B, W)  
*Gyrosigma variüstriatum* Hagelstein (B, T)  
  
*Hantzschia virgata* (Roper) Grunow (B, W)  
  
*Haslea wawrickae* (Hustedt) Simonsen (P, W)  
  
*Lyrella abruptoides* (Hustedt) Mann (B, W)  
*Lyrella approximata* (Greville) Mann (B, W) [note 34]  
*Lyrella atlantica* (Schmidt) Mann (B, C)  
 synonym: *Navicula lyra* Ehrenberg var. *atlantica* Schmidt  
*Lyrella clavata* (Gregory) Mann (B, C)  
*Lyrella clavata* var. *distenta* Hustedt (B, T)  
*Lyrella clavata* var. *indica* (Greville) Cleve (B, W)  
*Lyrella hennedyi* (W. Smith) Stickle et Mann (B, W)  
*Lyrella irroratoides* (Hustedt) Mann (B, T)  
*Lyrella lyra* (Ehrenberg) Karayeva (B, W)  
*Lyrella prae-texta* (Ehrenberg) Mann (B, C)  
  
*Mastogloia acutiuscula* Grunow var. *elliptica* Hustedt (E, T) [note 35]  
*Mastogloia angulata* Lewis (E, W)  
*Mastogloia apiculata* W. Smith (E, W)  
*Mastogloia baldjikiana* Grunow (E, T)  
*Mastogloia binotata* (Grunow) Cleve (E, W)  
*Mastogloia braunii* Grunow (E, C)  
*Mastogloia citrus* (Cleve) DeToni (E, T)  
*Mastogloia cribrosa* Grunow (E, T)  
*Mastogloia crucicula* (Grunow) Cleve (E, T)  
*Mastogloia decipiens* Hustedt (E, C)  
*Mastogloia dicephala* Voigt (E, T)

<i>Mastogloia elegans</i>	(E, C)
<i>Mastogloia erythraea</i> Grunow	(E, T) [note 36]
<i>Mastogloia erythraea</i> var. <i>biocellata</i> Grunow	(E, T)
<i>Mastogloia exigua</i> Lewis	(E, F)
<i>Mastogloia euxina</i> Cleve	(E, T)
<i>Mastogloia exilis</i> Hustedt	(E, T)
<i>Mastogloia fimbriata</i> (Brightwell) Cleve	(E, T)
<i>Mastogloia grunowii</i> Schmidt	(E, T)
<i>Mastogloia hustedtii</i> Meister	(E, T)
<i>Mastogloia lanceolata</i> Thwaites	(E, W)
<i>Mastogloia minutissima</i> Voigt	(E, C)
<i>Mastogloia omisa</i> Voigt	(E, T)
<i>Mastogloia ovalis</i> Schmidt	(E, T)
<i>Mastogloia paradoxa</i> Grunow	(E, T)
<i>Mastogloia pisciculus</i> Cleve	(E, T)
<i>Mastogloia pumila</i> (Grunow) Cleve	(E, C)
<i>Mastogloia pumila</i> var. <i>papuarum</i> Cholnoky	(E, C)
<i>Mastogloia pumila</i> var. <i>africana</i> Giffen	(E, C)
<i>Mastogloia pusilla</i> Grunow	(E, C)
<i>Mastogloia pusilla</i> var. <i>subcapitata</i> Hustedt	(E, T)
<i>Mastogloia schmidtii</i> Heiden	(E, T)
<i>Mastogloia smithii</i> Thwaites	(E, W) [note 35]
<i>Mastogloia splendida</i> (Gregory) Ralfs	(E, W)
<i>Mastogloia subaffirmata</i> Hustedt	(E, T)
<i>Mastogloia varians</i> Hustedt	(E, T)
<i>Navicula carinifera</i> Grunow	(B, W)
<i>Navicula clamans</i> Hustedt	(B, W)
<i>Navicula directa</i> W. Smith	(B, C)
<i>Navicula fromenterae</i> Cleve	(B, T)
<i>Navicula johanrossii</i> Giffen	(B, C)
<i>Navicula longa</i> (Gregory) Ralfs	(B, T)
<i>Navicula maculosa</i> Donkin	(B, C)
<i>Navicula normalis</i> Hustedt	(B, C)
<i>Navicula pennata</i> Schmidt	(B, C)
<i>Navicula platyventris</i> Meister	(B, C)
<i>Navicula pseudocomoides</i> Hendey	(B, C) [note 30, 41]
<i>Navicula pseudocrassirostris</i> Hustedt	(B, C)
<i>Navicula ramosissima</i> Agardh) Cleve	(B, C) [note 30]
<i>Navicula salinarum</i> Grunow	(B, W)
<i>Navicula scopulorum</i> Brébisson	(B, W)
<i>Navicula tripunctata</i> Müller) Bory	(B, F)
<i>Navicula yarrensis</i> Grunow	(B, T)
<i>Nitzschia amphibia</i> Grunow	(B, F) [note 38]
<i>Nitzschia brittonii</i> Hagelstein	(B, T)
<i>Nitzschia fonticola</i> Grunow	(B, F)
<i>Nitzschia frustulum</i> (Kützing) Grunow	(B, F)
<i>Nitzschia insignis</i> Gregory	(B, W)
<i>Nitzschia lanceolata</i> W. Smith	(B, W)
<i>Nitzschia lesbia</i> Cholnoky	(B, C)
<i>Nitzschia linearis</i> W. Smith	(B, F)
<i>Nitzschia lionella</i> Cholnoky	(B, C)
<i>Nitzschia longissima</i> (Brébisson) Ralfs	(B, W)
<i>Nitzschia lorenziana</i> Grunow var. <i>subtilis</i> Grunow	(B, C)

- Nitzschia martiana* (Agardh) Van Heurck (B, W) [note 30]  
*Nitzschia obtusa* W. Smith *forma parva* Hustedt (B, W)  
*Nitzschia palea* (Kützing) W. Smith *var. debilis* (Kützing) Grunow (B, F)  
*Nitzschia parvula* W. Smith (B, C)  
*Nitzschia quickiana* Hagelstein (B, T)  
*Nitzschia reversa* W. Smith (B, C)  
*Nitzschia rhopalodioides* Hustedt (B, C)  
*Nitzschia sigma* (Kützing) W. Smith (B, W)  
*Nitzschia sigma var. intercedens* Grunow (B, C)  
*Nitzschia socialis* Gregory (B, C) [note 39]  
*Nitzschia spathulata* W. Smith (B, W)  
*Nitzschia ventricosa* Kitton (B, T)  
*Nitzschia vidovichii* Grunow (B, C)
- Parlibellus berkeleyi* (Kützing) Cox (B, C) [note 40, 41]  
*Parlibellus delognei* (Van Heurck) Cox (B, C)  
*Parlibellus hamulifer* (Grunow) Cox (B, C)  
*Parlibellus tubulosus* (Brun) Cox (B, C)
- Petrodictyon gemma* (Ehrenberg) Mann (B, W) [note 42]  
 synonym: *Surirella gemma* Ehrenberg
- Petroneis granulata* (Bailey) Mann (B, W) [note 43]  
*Petroneis transfuga* (Grunow) Mann (B, T)
- Pinnularia gentilis* (Donkin) Cleve (B, F)  
*Pinnularia robusta* Hustedt (B, F)
- Plagiotropis lepidoptera* (Gregory) Kuntze (B, C)  
*Plagiotropis lepidoptera var. proboscidea* (Cleve) Reimer (B, F)  
*Plagiotropis seriata* (Cleve) Kuntze (B, C)
- Planothidium delicatulum* (Kützing) Round et Bukhtiyarova (E, F) [note 44, 45]  
*Planothidium hauckianum* (Grunow) Round et Bukhtiyarova (E, F)  
*Planothidium ellipticum* (Cleve) Round et Bukhtiyarova (E, F)  
 synonym: *Achnanthes lanceolata* Brébisson *var. elliptica* Cleve
- Pleurosigma aestuarii* (Brébisson) W. Smith (B, C) [note 46]  
*Pleurosigma angulatum* (Queckett) W. Smith (B, W)  
*Pleurosigma delicatulum* W. Smith (B, C)  
*Pleurosigma elongatum* W. Smith *var. gracilis* Grunow (B, C)  
*Pleurosigma formosum* W. Smith (B, C)  
*Pleurosigma intermedium* W. Smith (B, C)  
*Pleurosigma rigidum* W. Smith (B, W)
- Psammodictyon constrictum* (Gregory) Mann (B, W) [note 47]  
*Psammodictyon panduriforme* (Gregory) Mann (B, W)
- Pseudo-nitzschia delicatissima* (Cleve) Heiden (P, W)  
*Pseudo-nitzschia pseudodelicatissima* (Hasle) Hasle (P, W)  
*Pseudo-nitzschia pungens* (Grunow) Hasle (P, W)  
*Pseudo-nitzschia seriata* (Cleve) Peragallo (P, W) [note 48]
- Rhopalodia gibberula* (Ehrenberg) Müller (B, W)  
*Rhopalodia operculata* (Agardh) Håkansson (B, W)  
 synonym: *Rhopalodia musculus* (Kützing) Müller
- Stauroneis amorphoides* Grunow (B, T) [note 49]

<i>Staurophora amphioxys</i> (Gregory) Mann	(B, C)
synonym: <i>Stauroneis amphioxys</i> Gregory	
<i>Staurophora amphioxys</i> var. <i>producta</i> Grunow	(B, C)
<i>Surirella fastuosa</i> (Ehrenberg) Kützing	(B, W)
<i>Trachyneis aspera</i> (Ehrenberg) Cleve	(B, W)
<i>Trachyneis brunii</i> (Cleve) Cleve	(B, C)
<i>Tryblionella acuminata</i> (W. Smith) Mann	(B, W) [note 50]
<i>Tryblionella acuta</i> (Hantzsch) Mann	(B, C)
<i>Tryblionella coarctata</i> (Grunow) Mann	(B, W)
<i>Tryblionella granulata</i> Grunow) Mann	(B, C)
<i>Tryblionella granulata</i> var. <i>hyalina</i> Amosse	(B, T)
<i>Tryblionella marginulata</i> (Grunow) Mann	(B, C)
<i>Tryblionella marginulata</i> var. <i>didyma</i> Grunow	(B, C)

## NOTES

1. According to Håkansson (1996) some identifications of this taxon, including samples from Florida, are in reality *Cyclotella litoralis* Lange et Syvertsen.
2. The distinction between *Podosira* and *Hyalodiscus* is not clear (Round and co-workers, 1990); *P. stelliger*, for example, is frequently called *H. stelliger*.
3. According to Hasle (1979) many records of this species may be suspect; it appears to be primarily a benthic species, "possibly... as an epiphyte or trapped by branched larger algae...".
4. There is evidence that at colder temperatures this diatom becomes altered in its morphology and resembles *T. gravis* (Syvertsen, 1977).
5. This species was recently transferred to a new genus, *Calyptrilla*, later transferred again to *Neocalyptrilla* (Hernández-Becerril and Meave de Castillo, 1997).
6. The genus *Auliscus* is primarily fossil, and rarely seen alive; some have questioned whether it is solely fossil; at least *A. caelatus* is extant.
7. *Auliscus pruinosis* and *A. punctatus* are probably synonymous; see Sullivan, 1987)
8. This species has also been called *Triceratium alternans* and *Trigonium alternans*. The correct name depends on one's interpretation of the generic limits of the three genera involved.
9. The exact identity and validity of *C. brevis* is uncertain; see Rines and Hargraves, 1988.
10. Without the presence of resting spores (in *C. lorenzianus* only) it is difficult to separate *C. decipiens* from *C. lorenzianus* since morphological intergrades are common (see Rines and Hargraves, 1988).
11. There is no consistency to the naming of unicellular *Chaetoceros* species, and several names have been applied almost indiscriminately; see Rines and Hargraves, 1988.
12. This species is often reported in the literature, but has no taxonomic validity; it is difficult to say exactly what its identity is.
13. The differences between *C. peruvianus* and *C. pendulus* are not always distinct, and some authors have combined them (see Rines and Hargraves, 1988).
14. Round and co-workers (1990) have questioned whether *E. radiatus* is extant or only fossil.
15. Proper assignment to a genus depends on whether electron microscope examination shows the presence of ocelli (as in *Triceratium*), or pseudocelli (as in *Lampriscus*). See Round and co-workers, 1990, and Navarro, 1981.
16. The generic limits amongst *Amphipentas*, *Amphitetras*, *Biddulphia*, *Triceratium* and *Trigonium* are confused and complex: see Round and co-workers, 1990.
17. The structure of this species corresponds to Ehrenberg's genus *Amphipentas* (Sims, 2001)
18. If one considers the genus *Amphipentas* as valid, then this species would be the generitype (Sims, 2001)
19. This species has pseudocelli and non-loculate areolae, unlike the type species of *Trigonium*, and might be better placed in the genus *Sheshukovia* (P. Sims, pers. com., 8/01); see Round and co-workers, 1990.
20. Species in this genus were formerly placed in *Synedra*.
21. According to Sullivan and Wear (1995) this species may be misplaced in *Ardissonea*.
22. *Falcula* is primarily epizoic on marine zooplankton. Prasad and co-workers (1989) believe this is a mis-identification for *F. hyalina* Takano.
23. Some species in this genus were formerly placed in *Fragilaria*.

24. Round and co-workers (1990) place this species in *Microtabella*, an invalid name according to Navarro and Williams (1991)
25. Round and co-workers (1990) do not include this species in *Opephora*, but offer no alternative.
26. Although primarily an epiphyte on seagrasses, this species may also be abundant on the feathers of diving sea birds.
27. This species bears a resemblance to the recently described genus *Reimerothrix* (Prasad and co-workers, 2001), and may be a misidentification for that taxon. *Toxarium hennedyanum* is common in temperate coastal areas, whereas *R. floridensis* has been confirmed only from Florida Bay.
28. See Sala and co-workers (1998) for problems in identifying this species.
29. Most records throughout the world list *B. paxillifer* (or its synonym, *B. paradoxa*). It seems certain, however, that *Bacillaria* is made up of more than one species, and the one so common in the IRL is probably not *B. paxillifer*.
30. This is a diatom which forms foliose colonies, with the cells in mucilaginous tubes.
31. Round and co-workers (1990) do not distinguish between *Caloneis* and *Pinnularia*.
32. The genus *Climaconeis* appears to be more diverse in Florida than was previously evident (Prasad and co-workers, 2000).
33. Species of *Fallacia* were formerly in the genus *Navicula*.
34. Species of *Lyrella* were formerly in the genus *Navicula*, primarily in the 'Lyratae', variously called a subgenus, section, or simply, group.
35. Most species of *Mastogloia* are predominantly epiphytic, but may also exist as members of the epipelagic (sediment surface) community.
36. In some species of *Mastogloia* the number of internal marginal siliceous chambers (partecta) is related to valve length. Such is the case, for example, in *M. erythraea* and *M. smithii* (Novarino and Muftah, 1992).
37. This species may be planktonic, benthic, or symbiotic, and has been reported under a variety of names; see Round and co-workers (1999).
38. This is a large genus containing many species which are probably not closely related. A number of *Nitzschia* species have been transferred to other genera, e.g., *Psammodictyon* and *Tryblionella*.
39. The relationship between *N. socialis* and *Bacillaria paxillifer* is unclear. Individual cells of both taxa are similar, and it is becoming apparent that, contrary to conventional wisdom, *Bacillaria* is made up of several undescribed species.
40. *Parlibellus* includes a number of species formerly placed in the large and unwieldy genus *Navicula* (see Cox, 1988). The species listed here all occur primarily within mucilaginous tubes, sometimes branched.
41. According to Cox (1988), *Navicula pseudocomoides* Hendey is a synonym for *Parlibellus berkeleyi* (Van Heurck) Cox.
42. It is likely that many records of this species from subtropical and tropical waters are misidentifications of *P. patrimonii* Sterrenburg (see Sterrenburg, 2001).
43. Species of *Petronis* were formerly in the genus *Navicula* (see Round and co-workers, 1990).
44. The relationship between *P. delicatulum* and *P. hauckiana* is uncertain; see Patrick and Reimer, 1966.
45. Species of *Planothidium* were formerly in the genus *Achnanthes* (see Round and Bukhtiyarova, 1996).
46. Some authors (e.g., Patrick and Reimer, 1966) prefer to retain this species as a variety of *P. angulatum* (Queckett) W. Smith.
47. *Psammodictyon* was established by D.G. Mann (in Round and co-workers, 1990) to include the species from the Panduriformes section of *Nitzschia*.
48. *Pseudo-nitzschia seriata* is frequently a misidentified name for other species in this genus of very similar species (see Hasle and co-workers, 1996). These species potentially may produce domoic acid, a potent neurotoxin.
49. This species may be better placed in *Stauraphora*, which contains marine/brackish species with one plastid (Prasad and Silva, 2000). *Stauroneis* species usually have two plastids and are freshwater inhabitants. However, the IRL contains numerous adventitious freshwater species. I have not seen living cells, and so the chloroplast number is unknown.
50. *Tryblionella* consists of species formerly in the section Tryblionellae of the genus *Nitzschia*.

## IS THE CHEMICAL DEFENSE OF *EURYCOTIS FLORIDANA* A DETERRENT TO SMALL MAMMAL PREDATORS?

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**ABSTRACT.** *Adults of the subtropical cockroach Eurycotis floridana emit a defensive chemical spray from their abdomens consisting primarily of (E)-2-hexenal. Nymphs are similar in size to the adults, but lack the chemical defense. The ability of the defensive spray to repel predators has received relatively little study. We conducted feeding trials with two species of mice, Peromyscus gossypinus and P. polionotus, that are abundant in the natural habitats that support Eurycotis in central Florida, and potentially important predators on Eurycotis. We offered Eurycotis nymphs and adults to captive mice and recorded compared handling times among trials. Both species of mice were adept at handling nymphs but were visibly distressed when exposed to (E)-2-hexenal. Peromyscus polionotus proved largely unable to handle adult Eurycotis because of the inability of this mouse to deal with the chemical defense. In contrast, P. gossypinus dealt well with adult Eurycotis by thrusting the roach's abdomen into the substrate and feeding from the head end to avoid exposure to the chemical defense. We conclude that the chemical defense of Eurycotis is an effective deterrent to small mammal predators, but that at least some individuals of P. gossypinus adopt a behavior to neutralize that defense.*

**Key Words:** *Eurycotis floridana*, (E)-2-hexenal, *Peromyscus gossypinus*, cotton mouse, *Peromyscus polionotus*, oldfield mouse, chemical defense

THE WINGLESS cockroach *Eurycotis floridana* (Blattidae) is common in palmetto scrub, oak and pine forest, and suburban backyards in the southeastern United States (Brenner and Pierce, 1991). Adult *E. floridana* secrete a volatile chemical from their abdomens; nymphs are similar in size to adults but lack this chemical defense (Roth et al., 1956). At least 30 different compounds have been identified in the chemical secretion, with (E)-2-hexenal comprising roughly 90% of the organic phase (Farine et al., 1997, 2000).

*Eurycotis floridana* emit their secretion in response to disturbance, and the substance has been demonstrated to function as both a predator deterrent and an alarm pheromone (Farine et al., 1997). Eisner and co-workers (1959) determined that *Eurycotis* roaches could repel ants, beetles, spiders, frogs, and birds with their chemical defenses. Predators exposed to the spray were generally incapacitated for a short time, allowing the roach to escape unharmed. Certain predators,

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however, were only mildly (lizards) or apparently completely (praying mantids) undeterred by the chemical (Eisner et al., 1959).

In central Florida, mice of the genus *Peromyscus* are among the most abundant potential vertebrate predators on large, nocturnal, ground-dwelling arthropods (King, 1968; Wilson and Reeder, 1993; Whitaker, 1995). In Colorado short-grass prairie, for example, arthropods have been shown to comprise over 70% by volume in the diet of prairie deer mice (*P. maniculatus*) from March through June (Flake, 1973). Assuming Florida's *Peromyscus* spp. also consume large numbers of arthropod prey, one would expect the roach's chemical defense to be effective against these small mammals. Our objective in this study, therefore, was to test the efficacy of *E. floridana*'s chemical defenses against a potentially important, and untested, group of predators.

**STUDY AREA AND METHODS**—We conducted this study at the Archbold Biological Station in Highlands County, Florida (27° 10' 50" N, 81° 21' 00" W) from 22–30 March 1989. Habitats at Archbold include seasonal ponds, sandhills, flatwoods, scrub, and bayheads. Uplands are variably dominated by Florida rosemary (*Ceratiola ericoides*), slash pine (*Pinus elliotii*), sand pine (*Pinus clausa*), "Archbold" oak (*Quercus inopina*), saw palmetto (*Serenoa repens*), gallberry (*Ilex glabra*), and wiregrass (*Aristida stricta*) (Abrahamson et al., 1984).

We live-trapped cotton mice (*P. gossypinus*) and oldfield mice (*P. polionotus*) from the Station grounds and housed suitable individuals (i.e., adult males and non-lactating females) in 20 × 30 × 20 cm, clear plastic containers under natural light. Each container was filled to 2.5 cm with a mixture of sand and clay pet litter and topped with a wire mesh lid. The animals were given free access to water and dry dog food.

We obtained individual *E. floridana* from a laboratory research colony maintained by Dr. Thomas Eisner. Dr. Eisner also provided vials of (*E*)-2-hexenal, the primary component of *E. floridana*'s chemical defense, for use in our feeding trials.

Our laboratory experiments focused on a series of trials related to the handling time for different prey items offered to the captive mice. First, we examined the ability of the mice to subdue a generalized large, ground-dwelling insect (i.e., scarabaeid beetles collected from the Station grounds). Next, we assessed the ability of mice to handle *E. floridana* nymphs. We then quantified handling time for adult roaches with functional chemical weaponry. In two final feeding trials, we applied 1–2 drops of (*E*)-2-hexenal dorsally to posterior abdominal segments or to the head of roach nymphs. At the conclusion of the study, we released the mice to the area in which they were trapped.

In each trial, we placed the prey insect near the center of the mouse's container and recorded to the nearest minute (up to 30 minutes) the amount of time it took for the mouse to begin feeding. We conducted feeding trials under minimal light between the hours of 2030–2330 EST. We also checked containers approximately 90 min into the feeding trial and on the subsequent morning before 0700 hrs to assess the condition of any roaches that had survived the initial 30-minute observation period.

We used Mann-Whitney U tests to assess differences in predatory ability between the two species of mouse, and Kruskal-Wallis tests to identify differences in predatory efficiency among the feeding trials within species (Zar, 1984). Statistical analyses were performed with the Minitab 10.5 Xtra for the Power Macintosh statistical software package (Minitab, 1995).

**RESULTS**—We used three oldfield mice (two parous females and one non-reproductive male) and seven cotton mice (two non-reproductive males, four non-reproductive females, and one pregnant female) in our feeding trials. The cotton mice averaged larger ( $22.29 \pm 4.39$  g) than the oldfield mice ( $12.83 \pm 1.04$  g) (mean  $\pm$  SD).

We found no difference in handling time of scarab beetles ( $W = 47.5$ ,  $P = 0.194$ ) or *E. floridana* nymphs ( $W = 35.0$ ,  $P = 0.464$ ) between oldfield mice and cotton mice. The mice differed, however, in handling time of *E. floridana* adults ( $W = 28.0$ ,  $P = 0.018$ ) with handling time for oldfield mice (at least 720 min) longer than that for cotton mice ( $71 \pm 061$  min) (mean  $\pm$  SE). Only one of the three oldfield mice was able to prey upon an adult *Eurycotis*; roaches presented to the other two mice were still alive after 12 hrs when the feeding trials were terminated.

Adult *Eurycotis* presented to the mice sprayed in response to attacks from the mice. Those mice that were sprayed in the face rushed about, rubbed their snouts into the substrate, squinted their eyes, and vigorously groomed themselves for approximately 30–60 seconds. Both species of mice responded similarly to exposure to the roaches' defensive spray.

All three oldfield mice made initial lunges at the roach from the rear and were repelled by the chemical defense. Although their initial predatory advances came from the rear, at least some of the cotton mice altered their behavior after exposure to the roaches' chemical defense. Two cotton mice, after being sprayed in the face, approached their roaches head-on, and in one smooth movement, thrust the roaches' abdomens into the substrate and immediately began to feed on the heads. Other cotton mice may have ultimately used the same maneuver to subdue their roaches, but we did not specifically witness such behavior. All seven cotton mice consumed their adult roaches within two hours.

Next we offered *Eurycotis* nymphs to the mice, after first applying pure (*E*)-2-hexenal dorsally to the three posterior-most abdominal segments. Three of the cotton mice immediately thrust the abdomens of the nymphs into the substrates and began to feed on the heads. For the final feeding trial, we offered cotton mice roach nymphs with (*E*)-2-hexenal applied to their heads. Four of the seven mice quickly attacked the nymphs' heads. In each case, the mice were slowed and visibly distressed from encountering the chemical on the nymph heads, but all nymphs were eventually eaten.

We found no difference in handling time among any of the insects (beetles, roach nymphs, or roach adults) offered to cotton mice in any of the trials ( $H = 6.39$ ,  $P = 0.173$ ). In contrast, oldfield mice handled beetles and roach nymphs with relative ease ( $91 \pm 59$  min) (mean  $\pm$  SE) but took significantly ( $H = 8.77$ ,  $P = 0.033$ ) longer with adults (at least 720 min.).

DISCUSSION—Our observations suggest that the defensive chemical of *Eurycotis floridana* is irritating to the two *Peromyscus* species tested, and probably to other small mammalian predators as well. All mice that came in contact with the chemical were repulsed for a short time, during which the roaches moved away from the mice in the containers. We assume that after such an encounter in a natural setting, the roach would have an opportunity to seek shelter from its attacker. Also, would-be predators may altogether abandon their attempt to prey on *Eurycotis* after receiving a defensive spray in the face. This appeared to be the case for at least two of the oldfield mice in this study.

Oldfield and cotton mice differed in their ability to deal with the chemical defense of *Eurycotis*. Following exposure to (*E*)-2-hexenal, at least some of the cotton mice thrust their roach's abdomen into the substrate and began feeding on the head. No oldfield mice were observed to adopt this behavior, and oldfield mice were significantly less adept at handling adult *Eurycotis* than were the cotton mice. Because *Eurycotis* nymphs and adults are similar in size, we assume that the difficulty oldfield mice experienced in dealing with adult roaches was due to the chemical defenses of the adult roaches.

We did not observe the head-feeding behavior in cotton mice feeding on untreated nymphs. It is unclear if cotton mice are somehow triggered to engage in this behavior on detecting (*E*)-2-hexenal, or if our specific study subjects learned to use this behavior on *Eurycotis* after coming in contact with defensive, adult *Eurycotis*.

We conclude that the deterrent capability of *Eurycotis floridana*'s chemical defense to small mammal predators is dependent on the predator. We assume that any small mammal exposed to the defensive spray of *Eurycotis* would be at least temporarily deterred, and the roach would have an opportunity to escape. At least some cotton mouse individuals, however, adopt a behavioral strategy that minimizes their exposure to that defensive spray, and are efficient predators on *Eurycotis*. Thus the protection against small mammal predators afforded by the chemical defense of *Eurycotis* may be biologically significant, but it is not absolute.

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## ATTITUDE SURVEY ON COMPARATIVE ADVANTAGES OF PHOSPHOGYPSUM VERSUS BORROW PITS FOR ROAD FILL

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*ABSTRACT: Over 30 million tons of phosphogypsum (PG) are produced annually in Florida as a by-product of the production of phosphoric acid and derivatives. A previous study examined the environmental impacts of creating borrow pits to obtain fill for road building versus using phosphogypsum as a source of road fill. This study describes a survey that was conducted of approximately 50 qualified persons to identify as many issues and concerns as possible relative to this possible application.*

*Key Words:* Phosphogypsum, road fill, borrow pits, attitudes, issues

ONE consequence of the presence of the phosphate industry in Florida is the production of a significant amount of by-product. Over 30 million tons of phosphogypsum (PG) are produced annually in the state (Lloyd, 1985). Typically, this material is stacked indefinitely in engineered piles or stacks near phosphoric acid plants in central Florida. The piles are impressive in size: the smallest pile has about five million tons of PG (Lloyd, 1985), and a typical stack can be 200 feet high and cover 400–600 acres (FIPR, 1995). The total amount of PG stored was estimated to be 750–1000 million tons in Florida, Louisiana, Texas, Mississippi, North Carolina, Minnesota, and Wyoming (FIPR, 1995). Currently, 20 stacks are located in Florida, covering more than 6,000 acres, and totaling over 700 million tons of PG.

Phosphogypsum should be considered a resource. As was noted by Lloyd (2000), there is “almost universal agreement that it is better to try and find uses for wastes and by-products than to simply accumulate them”. The material is on average 92% pure gypsum, with principal contaminants of acids, insoluble phosphate materials, fluoride and trace amounts of radium (Borris and Boody, 1980).

Several ideas have emerged for uses of PG. One potential use is as road fill, and several roads and parking lots, built using PG as fill, are in daily use in Florida and Texas (FIPR and FSU, 1996). Phosphogypsum is classified as A-4 silty soil, rated as fair-to-poor as a subgrade material, but design standards of the Florida Department of Transportation permit A-4 silty soils to be used at least five feet below grade elevation and above the water table (FIPR and FSU, 1996).

The idea of utilizing phosphogypsum as a constituent in road fill material is not new. The concept was proposed at least twenty years ago, and several road

sections using PG have been in existence for over a decade (Chang, 1989, 1990; Chang and Mantell, 1990; Nifong and Harris, 1993; Taha et al., 1992). Controversy over the use of PG for road fill is also not new. Uncertainties with respect to public health prompted the United States Environmental Protection Agency (EPA) to promulgate a rule which places restrictions on the use of PG for various uses, including use in road construction.

Borrow pits have been utilized extensively in Florida as a source for road fill material. There are no federal restrictions specific to their use. There are, however, state and local land use-related controls which pertain to the excavation of borrow pits. Florida relies heavily on borrow pits for most of its road fill material, and most fill is generated via the excavation of open pits. Phosphogypsum could compete with the use of material from borrow pits, a practice that has been used since the time that Roman roads were constructed more than 2,000 years ago. A study examining the environmental impacts of PG versus borrow pits for road fill construction (Martin et al., 2001) concluded that the environmental impacts of PG were more favorable than those of borrow pits.

The problem of obtaining permission to use phosphogypsum is a problem that will ultimately be solved. In the meantime, it seemed helpful to have a better idea of the issues and problems as seen by informed persons, without expressing a biased (pro or con) opinion on the part of the interviewers, so a survey was undertaken to gain this information. The goal of this effort was to provide as complete a listing as possible of issues to be addressed by any organization that might seek to utilize PG in road construction. A summary of the survey results is included below; details concerning the issues raised and the questions asked are given elsewhere (Dooris and Martin, 2000).

*METHODS—General*—The first step in this process was to research the available literature on PG use in roadbeds and of borrow pit use. From this research, a list of potential issues was developed. This list was separated from the subsequent interview process, and was used as a post-interview check as to whether the interviews had: (1) resulted in new issues not uncovered during the literature research phase; and (2) succeeded in enumerating most if not all the issues uncovered during the research phase.

The second step was to identify approximately 50 individuals with some level of understanding of either PG use or of borrow pit use. The interviewers were careful not to attempt to “educate” any person being interviewed, as it was believed that any such effort could introduce bias into the results received (for example, if an interviewer was describing major constituents in PG, but failed to mention a given constituent, the person being interviewed might neglect to mention a potential issue regarding that constituent, assuming it was not present in PG). Given that no “education” of the person being interviewed was permitted, a person with no knowledge of PG or of borrow pits was not able to address the subject matter. This required that an initial listing of people who already had some knowledge of the matter be developed. This initial listing was derived from the literature research undertaken in the first step of the process. This list expanded when different people being interviewed provided the interviewer with additional people to speak with. The list was specifically designed to include individuals who might be classified as opponents as well as proponents of PG use. The list included scientists, environmentalists, engineers, public activists, and public health specialists. Again, the goal was to develop as complete a listing of potential issues as possible. Some 47 individuals were successfully contacted and actually interviewed. A list of types of persons interviewed is included in this report (Table 1).

TABLE 1. Categories of persons interviewed successfully.

Category	Number*
Engineers	3
Environmental Groups	5
Journalists/Information specialists	2
Phosphate Industry Personnel	3
Regulatory personnel	10
Transportation personnel	4
Scientists (biologists, ecologists, restoration specialists)	18
Not specified	3

\* The total may not add to 47 because of overlaps.

Every attempt was made to conduct the interviews in an unbiased manner. To facilitate the elucidation of issues by the person being interviewed, the person was assured that his/her name would *not* be associated with a particular issue in any way. People were more willing to proffer ideas freely, without fear of their name being placed next to an issue which might cause them embarrassment or problems. Also, the people being interviewed had their issues checked for accuracy by the interviewer during the interview (if the interview was conducted verbally) before the given issue was included in this report. All issues are provided exactly as relayed to the interviewer, so as to not risk inadvertent modifications of a given person's issue. If the issues were provided to us in written form, then they were included as received (with the exception of spelling/grammatical corrections if necessary and to delete words which would clearly serve to identify that person as the one making a given statement).

The third step in the process was to examine and summarize the issues and concerns received and compare those with the list developed in the initial step of the process. Only at this point in the process did the Institute for Environmental Studies (IES) project team modify any wording of any issue provided by an interviewee. We have made every attempt even at this step to not slant the meaning of a particular issue provided by an individual.

Categorizing the issues/concerns was done solely to assist the reader in maintaining a given line of thought. Categories are *not* listed in any type of prioritization as to importance. Certain people provided statements of position rather than elucidating issues. These were also included. While such statements do not add to the list of issues, they are deemed useful in providing insight into "perceptions" which may exist, and which may themselves need to be addressed in some manner.

*Instructions, protocols, and procedures used by the interviewers*—The interviewer related information to each person being interviewed: The interviewer explained that he/she was calling on behalf of the Institute for Environmental Studies at the University of South Florida. The whole project was looking at environmental and public health and perception issues pertaining to the use of borrow pits for road fill material and with the possible use of PG for roadbed material. The interviewee was asked to participate by helping to (1) identify individuals with knowledge of the subject matter, (2) solicit their opinions of the issues, (3) suggest interview questions and (4) encompass the environmental, public health, and perception aspects of borrow pits and/or PG use for road fills.

The interviewer asked the person being interviewed to think about what aspects of borrow pit use and/or PG use are of concern to them or which may be of concern to others. The interviewer asked them to relay those to us either in written or oral form, whichever way they felt most comfortable. If a verbal interview, then the interviewer wrote down the person's issues and questions. We presented or read to the person their final set of issues/questions before we placed them in the report, to make certain we had described the thoughts accurately.

The interviewer placed the person's name as an individual being interviewed in the report. However, the interviewer did not identify or associate that person's name with any given issue.

The person's questions/issues expressed could be general or specific. However, we informed people that the more specific the question they posed, the more likely it would be examined and answered later.

The interviewer could assist the person being interviewed in framing a question/issue as that person preferred it to be framed, but we did not dictate what questions are appropriate to ask, or what issues are appropriate to bring up.

In the initial contact with that person, the interviewer informed them that we would accept their ideas now, or if they preferred to think about it for a few days before the interview, arrange a time and date convenient for them to have the interviewer call them again. If the person preferred to put their issues and questions in writing, that was also acceptable.

The person on the phone at this point would elect to either set up a date and time for a phone interview, would decide to provide us their thoughts at that moment, or would choose to write down their thoughts and send them to us. Some preferred a face-to-face interview.

If the interview was oral, the interviewer concentrated on first understanding the question/issue being described. The interviewer listened carefully, making notes as he listened. After the person completed expressing a thought, the interviewer would stop and verbally restate that thought back to the person, so as to be certain he really did understand it. At that point, the interviewer would note the complete thought before continuing with the next thought.

When a person indicated that they had provided the interviewer with all they could think of, the interviewer offered to have him/her contact us if they have any other ideas after the interview.

The interviewer would read the questions/issues back to the person and obtain their concurrence with how each was written down. The interviewer would inform them that if their issue is modified following the interview, they will be contacted again with the modified wording. If not, we will state the issue as originally provided us.

Following the completion of all interviews, we compared the responses received to the list of issues we had identified from our own research into the subject matter. This list was compiled as a way of checking our research against the cumulative knowledge base of the people interviewed. If after all the interviews, there were still issues from our research list which had not been identified by one or more persons interviewed, our final report will identify those specific issues.

**RESULTS AND DISCUSSION**—It is important to understand that any attempt to summarize or synthesize opinions is bound to introduce some bias into the process. The reader is encouraged to study the individual comments and opinions provided elsewhere (Dooris and Martin, 2000) to obtain the clearest picture of the opinions of every person interviewed before reading the following summations.

Both borrow pits and PG had proponents and detractors. Comments which promote either borrow pit use or PG use may be read within the comments provided by the people interviewed, but are given in detail elsewhere (Dooris and Martin, 2000). Certain individuals pointed out that the crux of the problem was the lifestyle led in this country in that these alternatives to more/wider roads and green lawns would reduce the need for both borrow pits and PG production.

Borrow pits were characterized by most people as an ecological and aesthetic problem, with a potential to degrade or contaminate groundwater and/or surface water. PG use in road fill also had ecological and aesthetic aspects, but the major focus of most people centered around public health-related matters.

The ecological issues involving the use of borrow pits included: fragmentation of habitat; creation of steep-sided, deep water holes with minimal littoral zone (a “biological desert”); loss of natural soil horizon hence difficulties with re-establishment of natural vegetative communities on the sides (different pH, etc); loss of natural sheet flow; poor water quality; nuisance vegetation; reduction in biodiversity; disruption of bioenergetic pathways; loss of upland habitat; lowering of nearby

wetland water levels; lowering of nearby water table. Some of the concerns raised might be mitigated by the results of a related study (Martin et al., 2001).

The ecological issues involved in the use of PG for road fill involved mostly concerns over impacts to the health of organisms exposed to the material, either through direct contact, or weathering-related breakdown of the material. There was discussion of whether the pH and/or alkalinity of PG would assist or hinder efforts to revegetate roadsides with native species.

Water quality issues involving the use of borrow pits primarily involved the possibility of introducing contaminants into either groundwater or surface water via the loss of the natural filtering properties of the soil, and the presence of a "pit" conducive to disposing of unwanted materials.

Water quality issues involving PG for roadbed were related to public health concerns as well as possible exposure of ecological receptors. If PG stacks required liners to prevent contamination of groundwater, wouldn't the same type of concern hold for PG use as roadbed? Radium 226/228, radon, various metals, inorganics, and volatiles were mentioned by various individuals as possible concerns. Breakdown of the PG material over time and the subsequent release of contaminants was also an issue. Would breakdown/weathering actually create contaminants (such as sulfur dioxide, phosphoric acid, or other compounds)?

There were several public health and safety issues involving borrow pits. One involved the safety issue of people (especially children) falling into the pits. Another issue involved large trucks transporting the material. One individual raised the issue of bringing higher radioactive portions of the geologic strata to the surface via digging of borrow pits, and the resultant increased exposure of people to the higher radioactivity. Another talked of the increases in mosquitoes from having the pit act as a breeding ground.

Public health-related issues were perhaps the most frequently mentioned concern from those interviewed with respect to PG use in roadbed. The term "overriding" was used in this regard. Exposing people to constituents in PG in water and air was mentioned as an issue frequently. In addition to those constituents listed in the paragraph involving water quality, concerns were expressed over inhalation of the airborne PG crystals (the question was expressed in terms of an asbestos-like problem in the lungs), and the possibility that other potentially harmful materials may have been "dumped" in a gypsum stack in the past and inadvertently spread as part of the road fill.

Questions were asked regarding the relative structural integrity of borrow pit material versus PG in roadbed use. Which would last longer? Which would require less maintenance? One person suggested PG for use in pothole repair rather than for roadbed material. Questions were also asked regarding the relative economics of each.

Issues involving regulations of both borrow pits and PG use in roadbed were brought up by multiple persons. Several stressed the need for regulations to "restore" borrow pits to a more ecological and/or aesthetically attractive form following construction. Regulation of PG use centered on ensuring that public health is not threatened. A number of people spoke of the need for appropriate research

to be conducted by unbiased parties. Planning on a more holistic basis was recommended along with risk management and net ecosystem benefit type approaches to both borrow pit use and PG use.

It is our hope that the opinion survey will be useful in bringing significant issues to wide attention so that concerns can be addressed.

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## RECENT OCCURRENCE OF SAWFISHES (ELASMOBRANCHIOMORPHI: PRISTIDAE) ALONG THE SOUTHWEST COAST OF FLORIDA (USA)

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**ABSTRACT:** *Sawfish were once common in the southeastern United States, but became rare during the twentieth century before they were studied. They are protected from harvest in Florida, are considered "at risk of extinction" in North America by the American Fisheries Society, and listed as "endangered" by the World Conservation Union. Collections and observations of sawfish in southwest Florida from Charlotte Harbor to northern Florida Bay were documented by soliciting information from anyone who would encounter these fish (e.g., scientists, fishing guides, private citizens). We also circulated a poster (e.g., bait and tackle shops, boat ramps, fishing tournaments) that asked for anyone with any information on these fish since 1990 to contact us (by telephone, mail, or e-mail). Posters were distributed beginning in January 1999 and continue to be maintained from Port Charlotte, Florida (Charlotte County) south to Flamingo, Florida (Monroe County). Each person that had information was asked the same series of questions to determine the date and location of the encounter (collection or observation), estimated total length (ETL), and habitat characteristics. A total of 533 sawfish encounters that occurred between 1990 and 2001 were reported to us. Most sawfish encounters consisted of a single fish caught on hook and line, but groups of 2–20 similar-sized individuals were also reported. Neonates, juveniles, and sexually mature sawfish were found throughout the study area. These data indicate that the overall sawfish population is larger than previously thought; however, the majority of sawfish documented by this study were most likely sexually immature (89% < 3 m ETL). Thus, we support continued protection and conservation efforts and hope these efforts will allow the remaining sawfish populations to grow throughout their range. This study is the first survey on sawfish in Florida.*

**Key Words:** Charlotte Harbor, endangered species, Everglades, Florida Bay, largemouth sawfish, nursery, *Pristis pectinata*, *Pristis perotteti*, *Pristis pristis*, ray, smalltooth sawfish, Ten Thousand Islands

SAWFISH belong to a small group of elasmobranchs that usually occur in shallow coastal habitats in tropical and subtropical waters of the world, including estuaries and freshwater (e.g., Bigelow and Schroeder, 1953; Gunter, 1957; Thorson, 1974, 1982a). As the name implies, these fish possess an elongated, blade-like snout (rostrum) that has lateral, tooth-like denticles (rostral teeth). The rostrum (often referred to as the "saw") is easily noticed and is used during feeding and for defense (Breder, 1952; Bigelow and Schroeder, 1953). Sawfish are among the largest of the batoids and can grow to be 7 m long (Last and Stevens, 1994).

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Two species of sawfish (*Pristis pectinata* Latham, 1794 and *Pristis perotteti* Müller & Henle, 1841) have been historically recognized in the western Atlantic, although worldwide sawfish systematics are currently unsettled (Compagno and Cook, 1995). As currently understood, both western Atlantic species are found in similar habitats (Bigelow and Schroeder, 1953; McEachran and Fehhelm, 1998), but the largetooth sawfish, *P. perotteti* (recently referred to by some authors as *P. pristis*), breeds in and may prefer freshwater habitats (Thorson, 1976; Compagno and Cook, 1995). The ranges of both species have been reported to include Florida (e.g., Briggs, 1958), but there is no evidence that *P. perotteti* ever regularly occurred in the state. To our knowledge, only three specimens of *P. perotteti* have been documented in Florida: one from near Clearwater (Springer and Woodburn, 1960), one from Salerno (reported by S. Springer in Bigelow and Schroeder, 1953), and one from Key West (reported by S. Springer in Baughman, 1943). Thorson (1976) stated that *P. perotteti* "should probably be considered accidental in Florida" with its range typically south and west of the state (Baughman, 1943; Thorson, 1974). The vast majority of published records of sawfish collected in Florida refer to the smalltooth sawfish, *P. pectinata*, with hundreds having been historically reported from both coasts of the state (e.g., Bigelow and Schroeder, 1953).

Smalltooth sawfish were once common in Florida waters and were regularly reported in faunal surveys (e.g., Jordan and Swain, 1884; Henshall, 1891, 1895; Lönnberg, 1894; Evermann and Bean, 1898), but because of their morphology were particularly susceptible to fishing gears (e.g., gill nets, trawls) as bycatch (e.g., Henshall, 1895). Concurrent with sawfish population declines, these fishing methods were used extensively throughout the state for decades by commercial fishermen. Sportfishing activities also may have contributed to population declines because sawfish rostrums have historically been a popular curio item. These fishing activities, combined with limited reproductive potential (Simpfendorfer, 2000), probably had a significant negative impact on sawfish populations during the twentieth century (Snelson and Williams, 1981). Although no published studies specifically documented population decline in the United States, western Atlantic sawfish have been protected from harvest in Florida since 1992 (Florida Fish and Wildlife Conservation Commission, 1999), are currently considered "at risk of extinction" in North America by the American Fisheries Society (Musick et al., 2000), and are currently listed as "endangered" by the World Conservation Union (IUCN, 1996). The United States National Marine Fisheries Service (NMFS) was recently petitioned to add North American populations of the smalltooth sawfish to the List of Threatened and Endangered Wildlife under the Endangered Species Act of 1973 (United States National Marine Fisheries Service, 2000, 2001). If approved, *P. pectinata* would be the first elasmobranch to be listed as endangered in the United States.

With the exception of the work of Thomas B. Thorson (e.g., Thorson, 1974, 1976, 1982a, b), virtually nothing is known about sawfish biology anywhere in the world. In Florida, sawfish populations have apparently been extirpated from some estuarine systems (Schmid et al., 1988); however, specimens have been occasionally reported from fisheries surveys along the Gulf of Mexico coast (Adams and Wilson, 1995; G. R. Poulakis unpublished data). Because the location and

size of remaining sawfish population(s) are unknown in Florida, the goals of this study were to document the location of recent (1990–2001) collections and observations of sawfish in southwest Florida and to demonstrate that a reproducing population of sawfish still exists in the United States.

**MATERIALS AND METHODS**—Because of their unusual appearance and relatively large size, sawfish are easily recognizable to both scientists and non-scientists and tend to represent a memorable experience for those who encounter them. Collections and observations of sawfish in southwest Florida from Charlotte Harbor to northern Florida Bay were documented by soliciting information from anyone who would possibly encounter these fish. We also circulated posters ( $n = 72$ ) that displayed an image of a sawfish and asked for anyone with any information on these fish since 1990 to contact us (by telephone, mail, or e-mail). Older information and records from outside the study area were noted, but are not included here (records from the Florida Keys and Florida Bay will be reported in another paper). Posters were distributed beginning in January 1999 and continue to be maintained from Port Charlotte, Florida (Charlotte County) south to Flamingo, Florida (Monroe County). The posters were displayed where anglers and boaters would likely encounter them (e.g., bait and tackle shops, boat ramps, fishing tournaments). In addition to poster distribution, we attempted to obtain information about sawfish by contacting other fish biologists, fishing guides, guide associations, rod and gun clubs, scuba divers, mosquito control districts, and newspapers. Each person that had information was asked the same series of questions about their encounter(s). The survey included determination of the date and location of the encounter (collection or observation), estimated total length (ETL), and habitat characteristics (e.g., water depth, bottom-type). In cases where a person reported a length range for a fish, we used the midpoint of the range. Photographic documentation of encounters was obtained when available. All encounters were plotted on charts as exact points or in general areas depending on the detail of the available information. In most cases, the exact location of the encounter(s) could be determined during the interviews.

**RESULTS**—A total of 533 sawfish encounters that occurred in southwest Florida between 1990 and 2001 were reported to us (Figs. 1–3). We conducted a total of 168 interviews that documented 312 sawfish encounters. Of the sawfish encountered by non-scientists ( $n = 303$ ), 63% were captured with hook and line, 36% were observations, and 1% were captured by cast net. The remaining records came from Everglades National Park (ENP) from fisheries interviews completed by employees at the South Florida Natural Resources Center (SFNRC;  $n = 221$ ). Records provided by the SFNRC came from private sport fishermen or guides interviewed as part of a census developed to evaluate park-wide fishing effort and landings (1990–1999). No specific catch location information or length data was recorded for that census. Scientific records came from gill net and 183 m seine sampling in Charlotte Harbor by scientists at the Florida Marine Research Institute ( $n = 6$ ), longline sampling in ENP by scientists at Mote Marine Laboratory ( $n = 1$ ), gill net sampling in Rookery Bay National Estuarine Research Reserve by scientists at the Florida Department of Environmental Protection ( $n = 1$ ), and gill net sampling in Rookery Bay by visiting scientists ( $n = 1$ ).

Of the encounters where species was determined ( $n = 25$ ), all were *P. pectinata*. One specimen had rostral tooth counts between those typically used to separate *P. pectinata* and *P. perotteti* (21L, 22R). Unfortunately, the photographs of this specimen did not allow determination of fin placement or the presence of a lower caudal fin lobe.

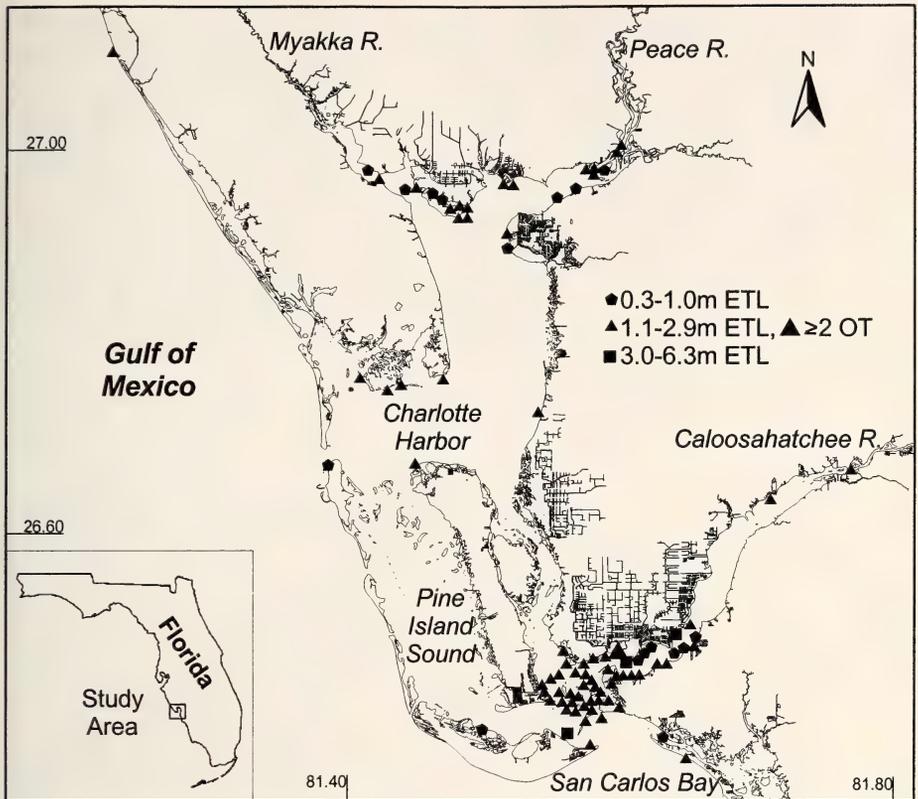


FIG. 1. Map of the greater Charlotte Harbor section of the southwest Florida study area where at least 100 sawfish were encountered between 1990 and 2001. Each small symbol indicates an encounter (catch or observation) with a single sawfish and each large symbol indicates  $\geq 2$  sawfish observed together (OT) in an estimated total length (ETL) size class. Eleven sawfish were reported from this section of the coast without specific location information.

Although size at maturity information is currently unavailable for *P. pectinata*, if we speculate that *P. pectinata* matures at approximately the same size as *P. perotteti* (ca. 3 m total length (TL) for both sexes; Thorson, 1976) or larger, the majority of the sawfish documented by this study probably had not reached sexual maturity when they were encountered (89% < 3 m ETL; Fig. 4). A total of 57 sawfish were very small, potentially young-of-the-year (0.3–1.0 m ETL) and a total of 35 were probably mature or nearly so ( $\geq 3.0$  m ETL).

Most sawfish encounters were reported as single fish being caught on hook and line, but there were several reports of multiple sawfish observed together. Small groups of 2–4 similar-sized individuals (0.9–2.7 m ETL) as well as larger groups of up to 20 similar-sized individuals (0.7 m ETL) were reported.

Water depths and bottom types were reported in many of the interviews we conducted. Of the interviews where water depth was estimated ( $n = 252$ ), fish from the smallest size class (0.3–1.0 m ETL) were found at an average depth of 1.1 m

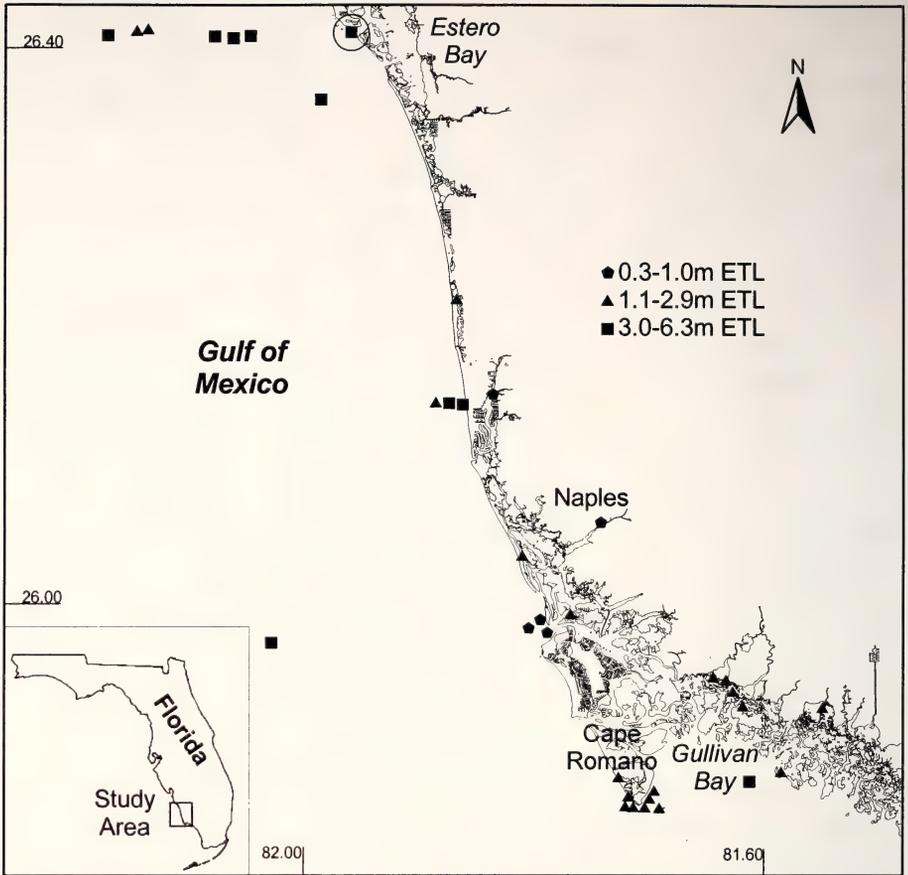


FIG. 2. Map of the Estero Bay to Cape Romano Island section of the southwest Florida study area where at least 35 sawfish were encountered between 1990 and 2001. Each symbol indicates an encounter (catch or observation) with a single sawfish in an estimated total length (ETL) size class. The circle indicates Big Carlos Pass where a 3.5 m ETL sawfish was caught six times (identified by its unique broken rostrum) from 18 August 1999 to 15 September 1999.

(range = 0.2–4.5 m), fish from the most commonly encountered size class (1.1–2.9 m ETL) were found at an average depth of 1.2 m (range = 0.2–8.5 m), and fish from the largest size class (3.0–6.3 m ETL) were found at an average depth of 3.5 m (range = 0.6–10.6 m). Of the interviews where bottom-type was noted ( $n = 255$ ), mud (60%), sand (30%), seagrass (6%), oysters (2%), and hard-bottom (2%) were reported. One encounter was reported near a freshwater upwelling.

*Greater Charlotte Harbor*—The greater Charlotte Harbor section of the coast spanned from ca. 27° 00' N to 26° 50' N and included Charlotte Harbor proper, Gasparilla Sound, Bull Bay, Turtle Bay, Matlacha Pass, Pine Island Sound, San Carlos Bay, and the Myakka, Peace, and Caloosahatchee Rivers (Fig. 1). A total of 100 sawfish encounters were reported to us from the greater Char-

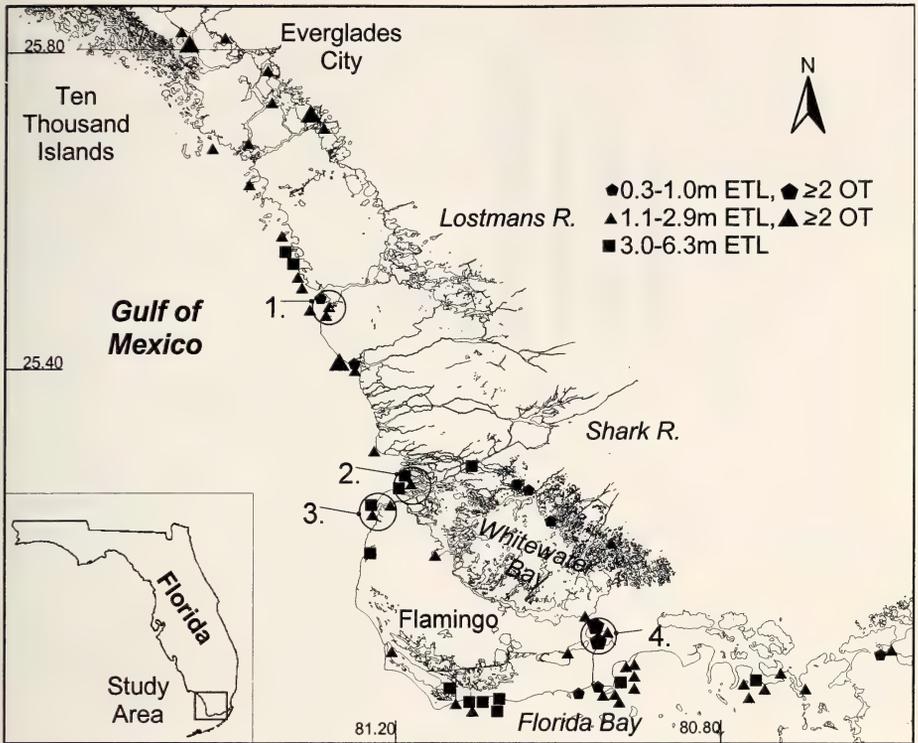


FIG. 3. Map of the greater Ten Thousand Islands section of the southwest Florida study area where at least 398 sawfish were encountered between 1990 and 2001. A total of 177 sawfish were reported from our interviews (1 without a specific location) and those data are represented here. Each small symbol indicates an encounter (catch or observation) with a single sawfish and each large symbol indicates  $\geq 2$  sawfish observed together (OT) in an estimated total length (ETL) size class. Note that the Everglades National Park boundary extends beyond this figure. 1 = The mouth of the Lostmans River where 63 sawfish have been caught from 1997 to 2001. 2 = The mouth of the Shark River where 16 sawfish have been caught from 1997 to 2001. 3 = The mouth of the Little Shark River where seven sawfish have been caught from 1997 to 2001. 4 = Coot Bay where ca. 23 sawfish have been encountered, including ca. 20 observed on one occasion.

lotte Harbor section of southwest Florida. The majority of the encounters reported in this section of the coast occurred near the mouth of the Caloosahatchee River (47%). The average size of sawfish encountered in the greater Charlotte Harbor section of the coast was 1.6 m ETL (range = 0.4–4.2 m ETL).

*Estero Bay to Cape Romano Island*—The Estero Bay to Cape Romano Island section of the coast spanned from ca. 26° 40' N to 25° 90' N (Fig. 2). A total of 35 sawfish encounters were reported to us from the Estero Bay to Cape Romano Island section of southwest Florida. The smallest number of sawfish encounters occurred in this section of the coast (7% of total), but the largest individual of the study was encountered in the Gulf of Mexico off Naples in June 1998 (6.3 m ETL). One 3.5 m ETL sawfish was captured at least six times near Big Carlos Pass

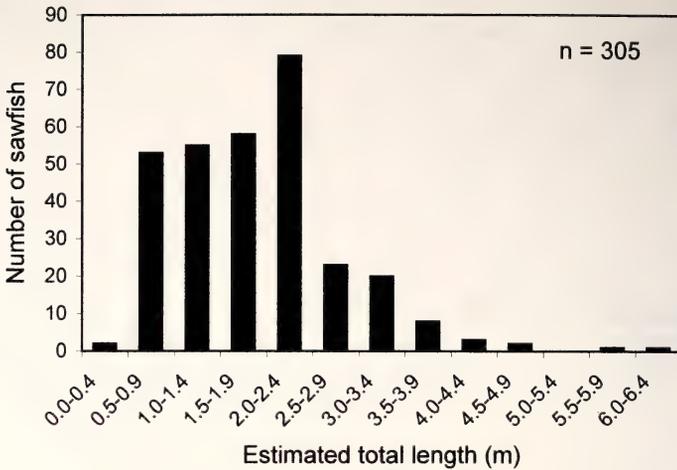


FIG. 4. Length frequency histogram of the estimated total lengths (ETL) of all sawfish reported with length data during the study ( $n = 305$ ). The 3.5 m ETL sawfish that was captured six times was included once. Seven sawfish were reported without length estimates.

from 18 August 1999 to 15 September 1999 and was identified by its unique broken rostrum. The average size of sawfish encountered in the Estero Bay to Cape Romano Island section of the coast was 2.4 m ETL (range = 0.8–6.3 m ETL).

*Greater Ten Thousand Islands*—The greater Ten Thousand Islands section of the coast spanned from ca. 25° 80' N to northern Florida Bay (ca. 25° 10' N) and included Whitewater Bay and ENP (Fig. 3). A total of 398 sawfish encounters were reported to us from the greater Ten Thousand Islands section of southwest Florida. Of the encounters reported in this section of the coast from our interviews ( $n = 177$ ), 58% occurred between the Huston River and the Little Shark River. Between 1997 and 2001, 63 sawfish have been captured at the mouth of the Lostmans River. The smallest sawfish encountered during the study (0.3 m ETL) was observed in Little Madeira Bay (northern Florida Bay) in April 2000. The average size of sawfish from our interviews in the greater Ten Thousand Islands section of the coast was 1.8 m ETL (range = 0.3–3.9 m ETL).

DISCUSSION—Literature from coastal fishery surveys, records from state fisheries management agencies, and records from institutions with marine holdings were examined by Adams and Wilson (1995) to determine the status of *P. pectinata* in the United States. They reported only 15 records from New York to Texas from 1953 to 1994 using this method. Not surprisingly, they suggested that “the species can no longer be considered a functional member of the nearshore coastal community of the northwest Atlantic.” The interview method used here provided substantially more information (and covered only a small part of the known range of sawfish in the United States) and minimally suggests that sawfish (probably *P. pectinata*) can be considered functional members of the nearshore

fish community in southwest Florida. Furthermore, this paper demonstrates that a reproducing sawfish population exists in the United States because neonates, juvenile, and sexually mature individuals have been recently encountered.

The interview method used here to document the occurrence of sawfish in southwest Florida produced valuable data, but had some obvious limitations. Not unexpectedly, very little detailed information such as confirmation of species or sex could be obtained as most of the records came from non-scientists. It was also impossible to determine recaptures unless a given fish was uniquely damaged (e.g., broken rostrum). However, documentation of the encounters, along with the location and size estimate data was useful for confirming the presence of these fish in the study area and establishing a baseline for future comparisons.

Although size at maturity information is currently unavailable for *P. pectinata*, Thorson (1976) found that male and female *P. perotteti* reached sexual maturity at ca. 3 m TL. If we speculate that *P. pectinata* has a similar or larger size at maturity, the vast majority of the sawfish encountered throughout the study area were immature. In addition, 57 of these immature fish (0.3–1.0 m ETL) were potentially young-of-the-year encountered near rivermouths (Myakka, Peace, Caloosahatchee) or well inside protected bays (e.g., Whitewater Bay). These observations suggest that coastal and protected estuarine habitats function as nursery areas for sawfish in southwest Florida. The presence of neonates also suggests that parturition occurred nearby. Thorson (1982a) reported that four immature sawfish (undetermined species) were taken in open waters of the Atlantic Ocean at depths as deep as 175 m, so some juveniles may also reside offshore as they grow to maturity.

Many larger shark species seasonally use estuarine or coastal habitats as nursery grounds to reduce neonate natural mortality and increase food availability for their young (Branstetter, 1990; Castro, 1993). Our data suggest that sawfish employ the same strategy in southwest Florida. Thirty-five potentially sexually mature sawfish were reported from the study area and most of these larger fish were caught in or closely associated with the deeper, open waters of the Gulf of Mexico. Because the largest individuals were rarely encountered by anglers that fished primarily inshore, mature sawfish may be very rare or present inshore only occasionally (perhaps to mate or pup). Future confirmation of the location of gravid females as well as more free swimming neonates will help improve our understanding of sawfish life-history in Florida.

Site fidelity has been documented for *P. perotteti* in Lake Nicaragua by tag-recapture data and site fidelity and use of a home range that expands with ontogeny has been documented for the lemon shark, *Negaprion brevirostris*, using telemetry (Thorson, 1982a; Gruber et al., 1988; Morrissey and Gruber, 1993). About 37% of the *P. perotteti* tagged by Thorson (1982a) were recaptured at the site where initial tagging took place, and large adult females moved the greatest distances away from the tagging site. In the present study, one 3.5 m ETL sawfish (identified by its broken rostrum) exhibited some site fidelity as it was captured near Big Carlos Pass (Estero Bay) on at least six occasions. Future tag-recapture, telemetry, or satellite tracking studies are needed to provide more information about the short- and long-term movements of sawfish in Florida.

Although most of the sawfish encounters documented by this study were reports of single fish being caught on hook and line, there were several reports of multiple sawfish observed together. Documentation of these social groups is further evidence that sawfish populations are larger than previously thought. Recent state protection and suitable remote habitats (e.g., Ten Thousand Islands, Everglades National Park) have probably contributed to the survival of *P. pectinata* in southwest Florida.

Like many elasmobranchs, sawfish have been vulnerable to overexploitation because they are long-lived and slow to reach sexual maturity (Thorson, 1982b; Hoening and Gruber, 1990). Even when mature, female sawfish may only reproduce every other year and give birth to a small number of young. As a result, demographic analyses have indicated that significant population growth may take several decades (Simpfendorfer, 2000). Thus, both western Atlantic sawfish species are currently protected from harvest in Florida and concern about their future by the American Fisheries Society and the World Conservation Union is justified (IUCN, 1996; Musick et al., 2000). We recommend and support continued sawfish protection and conservation efforts and hope these efforts will allow the remaining sawfish populations to grow throughout their range. Preliminary data indicate that sawfish are using the habitats of the Florida Keys and nearby Florida Bay. The authors are presently assessing the extent of sawfish encounters in these areas using the methods described in this paper.

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## COMPETITION BETWEEN *NEOTOMA FLORIDANA* AND *PEROMYSCUS GOSSYPINUS* ON KEY LARGO, FLORIDA

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**ABSTRACT:** *Competition between Neotoma floridana, Key Largo cotton mouse, and Peromyscus gossypinus, Key Largo woodrat, was investigated in tropical hardwood hammocks of Key Largo, Florida. A dynamic regression technique using time series data was used to determine if intra- and interspecific competition was occurring. Intraspecific competition was found in both species. P. gossypinus had a competitive effect on N. floridana, but there was no competitive effect of N. floridana on P. gossypinus.*

**Key Words:** Competition, cotton mouse, Key Largo, *Neotoma*, *Peromyscus*, woodrat

COMMUNITY ecologists have long sought to understand how species interact. One of the principal interactions of interest to ecologists has been competition. The interactions within and between species may affect the abundance and distribution patterns found in natural populations. Intraspecific competition causes a species to use a wider variety of habitats, but if a second species is added to the system there may be habitat selection where it did not previously exist (Rosenzweig, 1991).

Ecologists have used a variety of methods to determine competition coefficients within and between species. Competition is difficult to measure because of the spatial and temporal scales that are required for manipulative field studies and because there may be a considerable time lag between perturbation of a population and response to increased or relaxed competition. Schoener (1974) and Cromwell and Pimm (1976) developed a static regression technique that used census data and measures of habitat in order to determine competition coefficients. This technique used census data from multiple sites at one point in time where populations were assumed to be at equilibrium. Although used by mammalogists for a short period of time (e.g. Dueser and Hallett, 1980), the technique fell out of favor because of criticisms that there was a significant positive correlation between competition coefficients and population variance (Rosenzweig et al., 1985). In addition, inconsistent results were found when six variations in analysis were used to remove the effects of habitat heterogeneity, indicating that the competition coefficients determined with this technique were statistical artifacts of the analysis. Furthermore, Abramsky and co-workers (1986) and Pfister (1995) reported that this technique was unreliable with field experiments, but Fox and Lua (1996)

reported that it was reliable if species census data were standardized prior to calculating the regression parameters.

Pfister (1995) proposed the use of dynamic regression models to determine competition coefficients. Dynamic models use time series data to determine if per capita changes in one species are associated with abundance of other species (Seifert and Seifert, 1976; Berryman, 1991a, b). The dynamic regression method proposed by Pfister (1995) uses a linear difference model based on Lotka-Volterra differential equations:

$$\ln[N_1(t+1)/N_1(t)] = r[K_1 - N_1(t) - \alpha_{21}N_2(t)]/K_1 \quad (1)$$

The model uses time series data and does not assume that populations are at equilibrium, as does the static model. The equation has the form of a multiple regression with the dependent variable being the change in a species abundance from time  $t$  to  $t + 1$  and the terms on the right side representing the constant, the intraspecific competition component, and the interspecific competition component. Pfister (1995) demonstrated that dynamic regression models were consistent with results from experimental manipulations in an assemblage of intertidal fishes.

In this study, we chose to use the dynamic regression technique to determine if intra- and interspecific competition was occurring between *Neotoma floridana smalli*, Key Largo woodrat, and *Peromyscus gossypinus allapaticola*, Key Largo cotton mouse, two small mammals that are endemic only to Key Largo, Florida. This model was chosen because we had time series data from a few trapping grids and not single abundance estimates from multiple sites as required by the static model. The two species co-occur throughout the northern end of the island in tropical hardwood hammocks in various stages of succession. *Rattus rattus*, black rat, also occurs sporadically on the island and, therefore, was not included in the analyses. Models were created using data from all sites combined as well as individual sites. The combined model assessed the overall competitive interactions on Key Largo, whereas models from individual sites determined how abundance of con- or heterospecifics and succession affected competitive interactions.

**METHODS**—Live-trapping was conducted on four 10 × 10 grids in the 945 ha of tropical hardwood hammocks on Key Largo, FL. Grid 1 was a medium-aged hammock (last disturbed between 1940 and 1959), grid 2 was an old hammock (disturbed before 1926), grid 3 was a medium-aged hammock, and grid 4 was a medium-old hammock (last disturbed between 1926 and 1940).

Trapping stations on each grid were spaced 15 m apart for a total census area of 1.8 ha. Traps were baited with crimped oats. Each grid was live-trapped for three consecutive nights every four weeks from July 1996 until April 1998 except for grid 1, which was only trapped until July 1997 because of a problem with fire ants. Upon capture at a station, an animal was weighed, sexed, marked with an individual ear tag, and its location was recorded before being released. We used the Jolly-Seber method (Jolly, 1965) to estimate abundance for these species.

Abundance data from each trapping period were used to estimate competition coefficients using the dynamic model proposed by Pfister (1995). We created an overall model as well as individual models for each grid for both species.

**RESULTS**—Population size for *Neotoma floridana* was highest on grid 4 with 5.5 individuals, intermediate for grids 2 (3.0) and 3 (2.7), and lowest on grid 1

TABLE 1. Competition coefficients for *Neotoma floridana*.  $N_{NF}$  represents the intraspecific competition and  $N_{PG}$  represents the interspecific competition coefficient.

Dependent Variable	Location	$N_{NF}^a$	$N_{PG}^a$	F	$r^2$	P
$\ln(N_{NF+1}/N_{NF})$	All sites combined	-0.115**	-0.020*	12.68	0.281	<0.001
	1	-0.579*	0.048	3.94	0.529	0.071
	2	-0.144	-0.021	3.21	0.274	0.066
	3	-0.210**	-0.038*	7.32	0.478	0.006
	4	-0.122**	0.042	13.65	0.630	<0.001

<sup>a</sup> indicates significant partial regression coefficients at the following levels: \*  $P < 0.05$  and \*\*  $P < 0.01$ . P is the overall significance of the model.

with 1.7 individuals. *Peromyscus gossypinus* populations were high on grids 1 (21.1 individuals) and 3 (21.7) and low on grids 2 (14.0) and 4 (14.8).

The overall model for *Neotoma floridana* was significant and indicated that it was influenced by both intra- and interspecific competition (Table 1). On grids 1, 3, and 4 the competition coefficients indicate that *N. floridana* was engaged in intraspecific competition. On grid 3, *Peromyscus gossypinus* had a competitive effect on *N. floridana* according to the competition coefficient.

The overall model for *P. gossypinus* was also significant, but did not indicate a competitive effect of *N. floridana* on *P. gossypinus* at any of the individual sites (Table 2). The overall model indicated that *P. gossypinus* was affected by intraspecific competition on grids 2, 3, and 4.

DISCUSSION—A significant intraspecific competition coefficient was found on three of four of the grids as well as overall for both species. On grid 2, where the intraspecific competition coefficient approached significance in *Neotoma floridana*, abundance was intermediate for *N. floridana* and low for *Peromyscus gossypinus*. Intraspecific competition was found at other sites where *N. floridana* populations (grid 3) and *P. gossypinus* (grid 4) were similar in size to those of grid 2.

*Peromyscus gossypinus* was competing with *Neotoma floridana* on grid 3. On grid 3 *P. gossypinus* was abundant, as was the case on grid 1. There may be no effect of *P. gossypinus* on *N. floridana* on grid 1 because of the presence of

TABLE 2. Competition coefficients for *Peromyscus gossypinus*.  $N_{PG}$  represents the intraspecific competition and  $N_{NF}$  represents the interspecific competition coefficient.

Dependent Variable	Location	$N_{PG}^a$	$N_{NF}^a$	F	$r^2$	P
$\ln(N_{PG+1}/N_{PG})$	All sites combined	-0.035**	-0.148	18.86	0.367	<0.001
	1	-0.035	-0.075	5.01	0.589	0.045
	2	-0.041*	0.018	3.25	0.277	0.064
	3	-0.059**	-0.018	16.48	0.673	<0.001
	4	-0.033*	-0.007	2.86	0.264	0.086

<sup>a</sup> indicates significant partial regression coefficients at the following levels: \*  $P < 0.05$  and \*\*  $P < 0.01$ . P is the overall significance of the model.

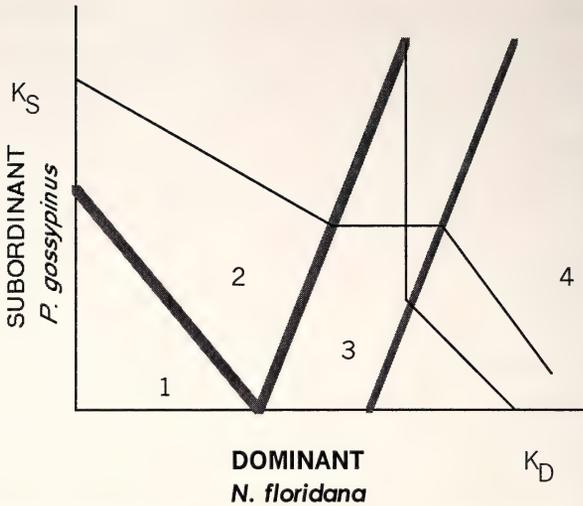


FIG. 1. Isolegs and Isoclines of a Shared-Preference Competition (Modified from Rosenzweig, 1991). The graph represents state space with the densities of the species as the axes.  $K_S$  is subordinate carrying capacity and  $K_D$  is dominant carrying capacity. Thick lines are isolegs that denote state space in a two habitat system. Regions are coded according to which habitat a species uses as follows: 1) both species select habitat 1; 2) the dominant species selects habitat 1 and the subordinate species selects both habitats; 3) the dominant selects habitat 1 and the subordinate selects habitat 2; and 4) the dominant selects both habitats and the subordinate selects habitat 2. Equilibrium occurs where the iso-clines for the two species cross in the state space where there is no overlap in habitat use (region 3).

*Rattus rattus* at that site. An analysis of competition between *R. rattus* and the two native species was not performed because they were all present only on grid 1. *R. rattus*, however, does influence how *Peromyscus gossypinus* uses space where they co-occur (Sasso, 1999).

Intraspecific competition was found in *Peromyscus gossypinus* overall and on grids 2, 3 and 4 and it approached significance on grid 1. Intraspecific competition was found at both high and low abundance of *P. gossypinus*.

*Neotoma floridana* was not found to have a competitive effect on *Peromyscus gossypinus*. *Neotoma floridana* are nowhere abundant on Key Largo, and the competitive effect must be strong for a rare species to have a significant effect on a common one (Pimm, 1985). As a cautionary note, due to the small sample sizes there is a danger of making Type I and Type II errors. However, this is a general problem inherent in studies of most endangered species.

Although the competition coefficients for the effect of *Peromyscus gossypinus* on *Neotoma floridana* were not large, they were negative and statistically significant, which is consistent with the basic ecology of these species. Because both species coexist, the competitive effect of one on the other cannot be too strong. If one species had a large competitive advantage, it would likely drive the other to local extinction. The lack of interspecific competition in most cases here does not imply that it is not occurring on Key Largo. *Neotoma floridana* and *P. gossypinus* are likely to have shared preferences in habitat use (Sasso, 1999).

Rosenzweig's (1991) work with isoclines and isolegs can be used to explain why competition is not detected in species with shared preferences. Figure 1 shows a shared-preferences isoleg and isocline graph. In region 3, the species isoclines interact and species select different habitats. Region 3 is the area of depressed competition. In that region, a change in the abundance of *Neotoma floridana* would cause no change in the abundance of *Peromyscus gossypinus* and vice versa. The competition models use a change in abundance to determine competition coefficients, therefore no interspecific competition would be detected if species were in region 3. This is what Rosenzweig (1991) calls the 'ghost of competition past', which is the absence or near absence of competition near the competitive equilibrium of two species.

In summary: (1) Intraspecific competition was found in both species; (2) At high abundance, *Peromyscus gossypinus* had a competitive effect on *Neotoma floridana* except when *N. floridana* numbers are low; (3) *Neotoma floridana* had no competitive effect on *P. gossypinus*; and (4) Shared preferences explain the apparent lack of interspecific competition. In the future, the competitive effects of *Rattus rattus* on *N. floridana* and *P. gossypinus* need to be determined. Additionally, experiments involving manipulations of abundance of *N. floridana* and *P. gossypinus* would be useful to confirm these findings and to assess if changes in abundance affect intra- and interspecific competition. Competition between the two species should be detectable if manipulations of abundance moved the species out of region 3 of shared-preferences state space. Unfortunately, the endangered status of these two species precludes such studies at this time.

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## DISTRIBUTION AND ABUNDANCE OF DOLPHIN-WATCHING COMPANIES IN FLORIDA

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**ABSTRACT:** *From May 1999 through March 2000, a thorough search for dolphin-watching companies was performed and recorded in a database to determine the abundance and distribution of commercial dolphin-watching companies throughout Florida. Companies were classified based on the level and/or type of dolphin-watching they performed. Frequency of tour operation per day and per season was analyzed for Pinellas County. More than 100 dolphin-watching companies were found in Florida. These results indicate dolphin watching is much more abundant throughout Florida than previously believed. Potential effects from high levels of dolphin watching are discussed.*

**Key Words:** *Tursiops truncatus*, bottlenose dolphin, commercial dolphin watching, harassment, cumulative impact, Marine Mammal Protection Act

DOLPHIN watching may seem like an activity that allows humans to “interact” with dolphins at a very low risk, but dolphin-watching companies have been observed conducting themselves in ways that are potentially harmful or disruptive for dolphins. Historical human/dolphin interactions included feeding wild dolphin populations to facilitate close encounters. Dolphins that became comfortable accepting handouts from humans and foraging near boats put themselves at risk of receiving harmful food and incidental boat strikes (NMFS, 1997; Wells and Scott, 1997). Feeding was later determined to be unhealthy for wild marine mammal populations and was banned by the National Marine Fisheries Service (NMFS) in 1991 (50 CFR 216); this final rule amended the Marine Mammal Protection Act, making it illegal to feed wild dolphins.

Some commercial dolphin-watching activities permit humans to enter the water and swim with wild dolphins; dolphins that have become accustomed to being fed by humans or are still illegally being fed will approach humans in the water; studies on swim-with-dolphin activities observed some interactions that were determined unsafe for both the animals and the humans (Samuels and Bejder, 1998; Seidemen, 1997). Operators who complied with the ban on feeding began dolphin-watching tours that closely approached pods so passengers could observe the animals and take pictures. Bottlenose dolphins react to close approaches from boats by fleeing, diving for prolonged periods of time, sheltering their young, and changing their original behavior (Richardson and Wursig, 1997). Dolphin watching as commercial activity has the potential for unanticipated effects; cumulative

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impacts from multiple dolphin-watching vessels must also be taken into account when considering the level of disturbance inflicted upon a pod of dolphins.

A 1993 report to the International Whaling Commission summarized the extent of whale and dolphin watching throughout the world (NMFS, 1993). Several states in the Southeastern United States (North Carolina, South Carolina, Florida and Texas) reported limited dolphin-watching activities (primarily of the bottlenose dolphin, *Tursiops truncatus*) taking place in coastal waters, shallow bays and estuaries as early as the 1970s. In 1983, four commercial dolphin-watching companies were operating in the southeastern United States; by 1993, the number of companies had grown to 25. Estimated growth for the dolphin-watching industry over the next year was predicted to be negative 10 to 20% due to the 1991 ban on feeding wild dolphins (50 CFR 216). Long term growth for 2000 was predicted to be stable after the initial reduction in companies (NMFS, 1993).

The objectives of this study were to determine the extent of commercial dolphin watching throughout Florida and discuss the potential impacts high levels of dolphin watching may have upon the species.

**METHODS**—We began the study by developing a database to determine the number and distribution of the dolphin-watching companies. No previous list or database of dolphin-watching companies was available. We contacted the Chamber of Commerce in each major city along the coast to solicit information and brochures for dolphin-watching tours in their areas. Internet searches were conducted for major cities that had local attractions posted online. Any company that used an image of a bottlenose dolphin or mentioned the possibility of sighting bottlenose dolphin in their advertising was included in the database. Due to local knowledge and close proximity to coastal cities in Pinellas County, the county was searched most thoroughly and will be used as a model region. In Pinellas County, we also visited hotels and tourist information centers to collect fliers and brochures about dolphin-watching companies.

To determine distribution, we divided Florida into 11 regions by counties (Fig. 1). Region 1 includes Escambia, Santa Rosa, Okaloosa, Walton, Bay and Gulf County. Region 2 includes Franklin, Wakulla, Jefferson, Taylor and Dixie County. Region 3 includes Levy, Citrus, Hernando and Pasco County. Region 4 consists only of Pinellas County. Region 5 is Manatee and Sarasota County. Region 6 includes Charlotte, Lee and Collier County. Region 7 includes only Monroe County. Region 8 is Dade and Broward County. Region 9 includes Palm Beach, Martin and St. Lucie County. Region 10 includes Indian River, Brevard, Orange and Volusia County. Region 11 includes Flagler, St. Johns, Duval, and Nassau County.

The database was designed in Microsoft Excel. We recorded the name of the tour company, the county in which the company was located, the company's address and phone number, the name of the boat and captain, cost per adult passenger, number of tours per day, length of tour, and any specific comments/information regarding sighting frequency or advertising tactics (Appendix 1). Not all the above information was available for each company; only complete information was used for analysis in this study.

The companies were then classified by the tour's activities and level of dolphin watching that was likely to occur on the tour. A company was classified as Type 1 if it operated primarily as a dolphin-watching cruise. A Type 2 classification was for tours that combined dolphin watching and swim-with-dolphin activities. A Type 3 company was an eco-tour, nature tour, island ferry, or charter fishing vessel that mentioned the possibility of dolphin sightings during their tour. Lastly, Type 4 was for a charter vessel service or personal watercraft rental company that allowed the customer to design a personal itinerary; their advertisement mentioned dolphin watching and/or swimming as an option.

**RESULTS**—We found more than 100 companies in Florida that either advertise dolphin watching or mention the possibility of sighting dolphins on their tour.

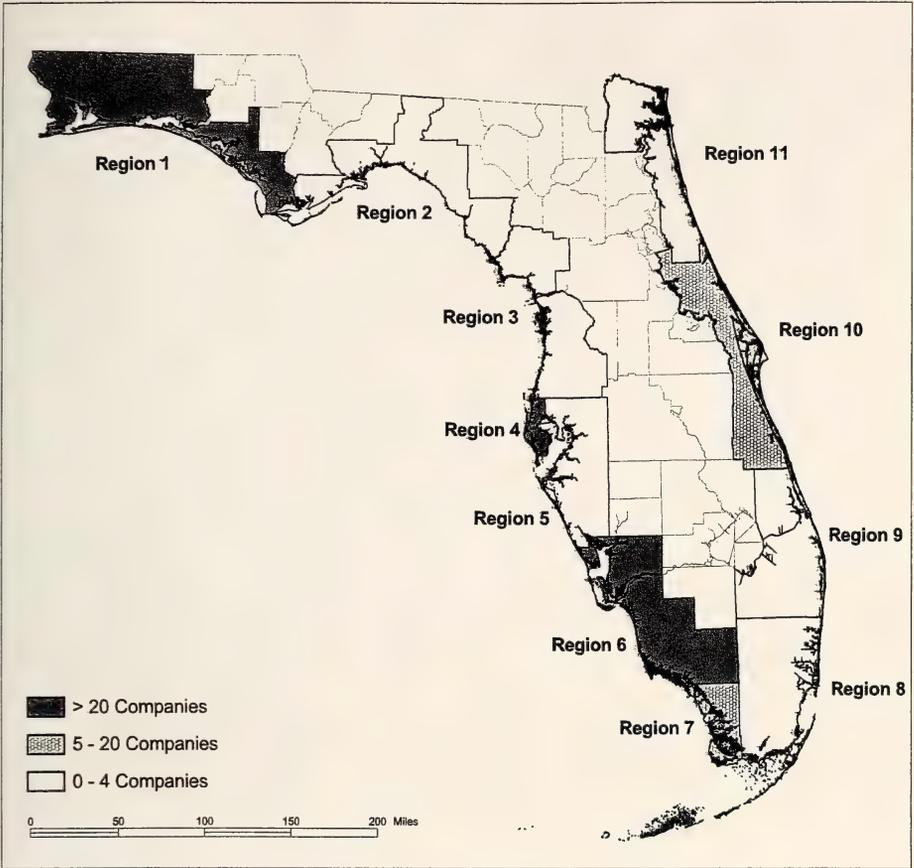


FIG. 1. The coastal counties in Florida were divided into 11 regions. The regions have been shaded to represent the total number of dolphin-watching companies in each.

Dolphin watching was found in nine of the 11 regions (Fig. 2). Within Region 1, there are 27 companies, located mainly in Panama City, Panama City Beach, and Destin. Only one dolphin watching company was found in Region 3, on Cedar Key. Region 4, which includes only Pinellas County, has 24 companies. The companies are located in Tarpon Springs, Clearwater, St. Petersburg Beach, and St. Petersburg. Three dolphin-watching companies are operating in Region 5 out of Sarasota, Bradenton and Long Boat Key. Within Region 6, there are 25 companies located in Fort Myers, Fort Myers Beach, Placida and Boca Grande. Region 7 has 13 companies operating primarily out of Key West. Region 8 has only one company; Region 9 has two companies in Stuart and Fort Pierce. Region 10 has seven companies operating out of Melbourne, Sebastian, Cocoa Beach and Titusville.

Fourteen of the 24 companies in Pinellas County (Region 4) are Type 1, indicating that they are specifically dolphin-watching companies. Nine of the remaining companies are Type 3 meaning that they are eco-tours, nature tours, island

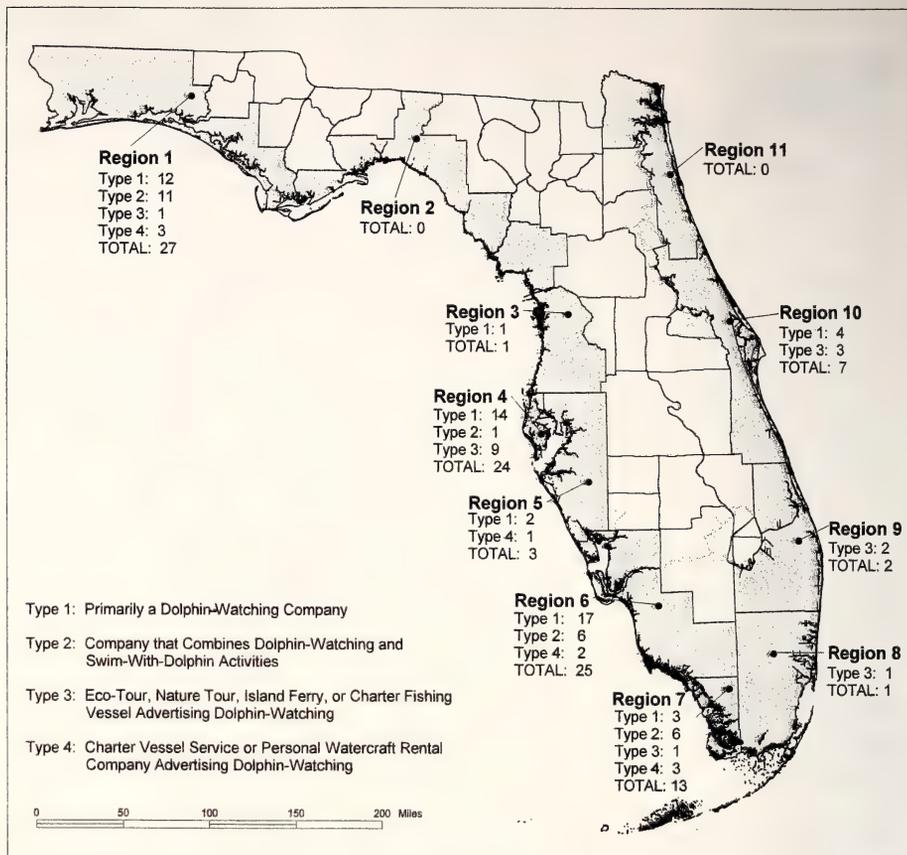


FIG. 2. The 11 regions are shaded and labeled with a breakdown of the abundance of each type of dolphin-watching company found within the region.

ferries, or charter fishing vessels that mentioned the possibility of dolphin sightings during their tours. One company is Type 4 indicating that it is a boat/jets-ski rental operation that tells customers to watch dolphins. No swim-with-the-dolphin companies were found operating in Pinellas County.

In Region 4, the 14 companies that offer primarily dolphin-watching tours cumulatively run 48 tours per day; all of the companies offer tours seven days per week during the summer. This calculates to be 4,416 tours during the summer months of July, August, and September when a study by Weigle (1990) determined the density of dolphins per square kilometer to be the highest around Pinellas County. Some of these tour companies operate nearly year-round but on reduced frequency of tour schedules during the off-peak months.

**DISCUSSION**—The results show that dolphin watching is a widespread activity throughout Florida. Before we developed the database of dolphin-watching companies, members of the scientific community and the National Marine Fisheries

Service (NMFS) had only rough estimates of how many companies were in operation. The industry has grown dramatically beyond NMFS' predictions made in 1993 that expected fewer than 25 companies to be operating throughout Florida in the year 2000 (NMFS, 1993). The current number of dolphin watching companies in Pinellas County alone nearly exceeds the number of companies in the entire southeastern U.S. seven years ago.

Based upon our calculations, the primary dolphin-watching companies in Pinellas County are offering 48 tours every day during the summer. Additionally, there are 10 other companies that incorporate dolphin watching into their business even though it is not the principal reason they operate their tour. The potential for impact on the dolphins based strictly on the number of tours offered per day is extremely high.

Understanding the extent to which dolphin watching is currently occurring is an important consideration when planning for new management of the dolphin-watching industry. To successfully manage and enforce dolphin watching, NMFS must develop a means of tracking how many dolphin-watching vessels are in operation. Not only will cumulative impact occur from the frequency and length of time the dolphins are in contact with tour boats, but the potential for harassment, injury or even death increases with the quantity of tour boats operating. Either the number of dolphin-watching boats in operation or the number of tours permitted per day needs to be limited for each region.

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## APPENDIX

Database of Dolphin-Watching Companies in Florida as of March, 2000. Only the Region Number, Company Name, Location and Tour Type are shown. Type 1 is primarily a dolphin-watching cruise, Type 2 is a company that combines dolphin-watching and swim-with dolphin activities, Type 3 is either an eco-tour, nature tour, island ferry, or charter fishing operation that mentions the possibility of dolphin sightings during their tour, and Type 4 is a charter vessel company or personal watercraft rental company that allows the customer to design a personal itinerary and mentions dolphin watching and/or swimming as an option. Duplicate company names indicate the company operates tours out of multiple locations.

Region	Company Name	Location	Type
1	A-Fin Charters	Panama City	4
1	AJ's Sea Blaster	Destin	1
1	Ashley Gorman Shell Island Sightseeing Cruises	Panama City	2
1	Beach Boys Charter Fishing	Panama City Beach	2
1	Capt. Anderson's III	Panama City	1
1	Dolphin and Sunset Cruises-Moody	Destin	1
1	Dolphin Cruise/Southern Star	Destin	1
1	Glass Bottom Boat	Destin	1
1	Great Adventure Water Sports	Panama City Beach	1
1	Harbor Cove Charters	Destin	1
1	Hathaway's Boat Rentals and Wave Runner Tours	Panama City Beach	2
1	Hydrospace Dive Shop	Panama City Beach	2
1	Island Star Sightseeing	Panama City	1
1	Island Wave Runner Tours	Panama City	1
1	J&B Marine Pontoon Rentals	Panama City	4
1	Miss Ashley Snorkeling Trip	Panama City Beach	2
1	Osprey's Excursions	Destin	1
1	Panama City Beach Sports/St. Andrews State Park	Panama City Beach	1
1	Panama City Watersports	Panama City	2
1	Prince of Tides	Panama City Beach	2
1	Real Time Charters	Panama City	4
1	Scotty Boat Rentals	Panama City	2
1	Sea Screamer	Panama City Beach	1
1	Shell Island Shuttle	Panama City Beach	2
1	Shell Island Wave Runner Tours	Panama City Beach	2
1	Snorkel and Swim with Dolphins Safari	Panama City	2
1	Swim with the Dolphins	Panama City Beach	2
3	Island Hopper Scenic Cruises	Cedar Key	3
4	Capt. Frank's Island Taxis	Saint Petersburg	1
4	Capt. Mike's Watersports	St. Petersburg Beach	3
4	Captain Bill's Destiny Yacht Charters, Inc.	Saint Petersburg	1
4	Captain Dave's Watersport's Center	St. Petersburg Beach	3
4	Captain Memo's Pirate Cruise, Inc.	Clearwater Beach	3
4	Caribbean Queen	Saint Petersburg	1
4	Dolphin Landings Charter Boat Center	St. Petersburg Beach	1
4	Egmont Key Island Adventures	St. Petersburg Beach	3
4	Hubbard's Sea Adventures, Inc. Dolphin Watch	Madeira Beach	1
4	Island Hopper Excursion Docks	Clearwater Beach	1
4	Island Wind Tours	Tarpon Springs	3
4	Jack's Boat Rentals	Madeira Beach	1
4	Kai Lani	Clearwater Beach	1
4	Little Toot	Clearwater Beach	1
4	Mar-Chelle II	Clearwater Beach	3

## APPENDIX Continued.

Region	Company Name	Location	Type
4	Sea Life Safari Cruise	Clearwater Beach	3
4	Sea Screamer	Clearwater Beach	1
4	Shell Key Shuttle	St. Petersburg Beach	3
4	Show Queen Cruises	Clearwater Beach	3
4	Star of the Croix	Madeira Beach	1
4	The Original Dolphin Encounter Cruise	Clearwater Beach	1
4	The Queen Fleet	Clearwater Beach	1
4	Tierra Verde Boat Rentals	Saint Petersburg	4
4	Windjammer Cruises	Clearwater Beach	1
5	Mahina La Catamaran Adventures	Bradenton	1
5	Miss Explorer	Sarasota	4
5	Sarasota Bay Explorers	Sarasota	1
6	Adventure Water Sports	Fort Myers	1
6	Boca Boat Cruises and Charters	Boca Grande	3
6	Calusa Coast Outfitters	Fort Myers Beach	1
6	Captiva Cruises	Captiva Island	1
6	CRS Beach Service	Fort Myers Beach	1
6	Double Sunshine	Naples	1
6	Factory Bay Marina Airboat Tours	Marco Island	3
6	Grande Tours, Inc.	Placida	1
6	"Gulf Breeze" Eco-History Tour	Fort Myers Beach	3
6	Holiday Water Sports, Inc.	Fort Myers Beach	1
6	Holiday Water Sports, Inc.	Fort Myers Beach	1
6	Jug Creek Cruise Boat	Bokeelia	4
6	Le Barge	Sarasota	1
6	Mid Island Water Sports	Fort Myers Beach	1
6	Mid Island Water Sports	Fort Myers	1
6	Rebel Water Sports	Fort Myers Beach	1
6	Rebel Water Sports	Fort Myers Beach	1
6	Sail Away Charters	Marco Island	3
6	Sand Dollar Nature and Sunset Cruises	Fort Myers Beach	1
6	Sanibel Island Cruise Line	Sanibel	1
6	Sanibel Marina	Sanibel Island	3
6	Tropic Star Cruises	Bokeelia	3
6	Wind and Watersports Adventures, Inc.	Fort Myers Beach	1
6	Wind and Watersports Adventures, Inc.	Fort Myers Beach	1
6	Yacht Cruises	Cape Coral	4
7	Boomer Watersports	Key West	4
7	Capt. Vicki Impallomeni	Key West	2
7	Dailey Discovery	Key West	2
7	Dolphin Watch	Key West	2
7	Easy Day Charters	Key West	2
7	Gale Force Charters	Key West	4
7	Keys Adventure Tours	Key West	1
7	Lost World Expeditions	Key West	3
7	Low Key Charters	Key West	2
7	Schooner Reef Chief	Key West	4
7	Wild About Dolphins	Key West	1
7	Wild Fly Charters	Key West	1
7	Wild Quest	Key West	2

## APPENDIX Continued.

Region	Company Name	Location	Type
8	Sea Screamer	Pompano Beach	3
9	Cajun Boat Tour	Fort Pierce	3
9	Island Princess Cruises	Stuart	3
10	Fun Day Discovery Tours	Melbourne	1
10	Fun Family Fishing and Sightseeing Trips	Cocoa Beach	3
10	Inlet Explorers	Melbourne Beach	3
10	Lady Dolphin Indian River Cruises	Sebastian	1
10	Osprey Outfitters	Titusville	3
10	River Queen Cruises	Sebastian	1
10	Sea Pirate River Cruises	Melbourne	1

## PERSISTENT PALMETTOS: EFFECTS OF THE 2000–2001 DROUGHT ON *SERENOA REPENS* AND *SABAL ETONIA*

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**ABSTRACT:** *The severe and prolonged drought of 2000–2001 that affected Florida and the rest of the southeastern United States provided a unique opportunity to examine the impacts of drought on the survivorship and growth of Serenoa repens and Sabal etonia. In addition, a dry-season wildfire that occurred at the height of the drought enabled us to observe the combined impacts of drought and fire on a subset of adult palmettos and two cohorts of seedlings. On average, all populations of adult palmettos and the majority of individuals lost mass during the drought; however, the survivorship of adult palmettos was little affected by either drought or the combination of drought and an intense wildfire. Only 2 of the 937 monitored adult palmettos alive prior to the drought died; both were smaller-than-average-sized Sabal and one was severely burned during the drought. The greatest impact observed was on palmetto seedling survival in scrubby flatwoods where cumulative rates of seedling mortality were more than tripled following the drought. Nevertheless, 55% of a 1989 scrubby flatwoods cohort and 70% of a 1989 flatwoods cohort continue to survive after nearly 13 years, a severe drought, and an intense wildfire. Both seedling and adult Serenoa and Sabal show extraordinary persistence and tolerance to severe drought and intense dry-season wildfire.*

**Key Words:** drought, fire, Florida, palmetto, *Sabal etonia*, *Serenoa repens*, survivorship

THE southeastern United States experienced a severe and prolonged drought during 2000–2001. The 12-month-period from September 1999 to August 2000 was the driest such period across the Southeast since national records began in 1895 (NOAA National Climatic Data Center, 2002a). The persistence of this drought had a cumulative effect, which led to a rapid intensification of the drought's severity. The Palmer Drought Index for the Southeast region during this period reached intensity levels comparable to the severe drought of the 1950's, and second only to the drought of 1925.

Within Florida, dry conditions preceded the 2000–2001 drought with below-average precipitation falling statewide during April, May, June, August, October, and December of 1998 and during February, March, April, May, July, August, November, and December of 1999. Furthermore, only August 2000 and March 2001 had above-average precipitation during the 15-month period between January 2000 and March 2001. The April 2000 to March 2001 period was the 7th driest on record for Florida (NOAA National Climatic Data Center, 2002b). The Tampa Bay region, for example, experienced its fourth driest dry season on record between October 1999 and May 2000 but this period of drought was preceded by the second driest dry season on record beginning in October 1998

through May 1999. Additionally, May 2000 was the driest May in Tampa since records began in 1890.

The persistence of the drought was also recorded in Highlands County at Archbold Biological Station (ABS). The ABS weather station recorded the first 20-month period with well-below average precipitation (17.8 cm or more below the 1932–2001 mean) since ABS weather records began in 1932. The 20-month period of October 1999 to May 2001 accumulated only 109.5 cm of precipitation versus a long-term mean of 189.5 cm precipitation (58% of normal). The June–September (rainy season) long-term mean at ABS is 81.1 cm of precipitation but the rainy season of 2000 accumulated only 47.5 cm of precipitation (59% of normal). The October–May (dry season) long-term mean at ABS is 54.2 cm of precipitation, but only 35.4 cm fell during the dry season from October 1999 to May 2000 (65% of normal), and only 26.6 cm from October 2000 to May 2001 (49% of normal).

There were many consequences of this prolonged and severe drought. Across the south-central and southeastern United States, the drought caused an estimated \$4 billion in losses to agriculture and related industries (NOAA National Climatic Data Center, 2002c). The *Florida Weekly Crop and Weather Report* (April 16, 2000) reported that most water holes and some wells went dry in central Florida, while brush fires were active in west-central Florida. The *Miami Herald* (May 18, 2000) reported that State authorities had banned outdoor burning across Florida—except for backyard and campground grills as the “severe drought prompted fears of wildfires and revived memories of the 1998 scorching that uprooted thousands of Floridians.” There were numerous reports of tree mortality during 2000–2001. For example, Florida forestry officials estimated losses of up to 4 million trees in 2000; four times normal (NOAA National Climatic Data Center, 2002d). At ABS, considerable sand pine (*Pinus clausa*) mortality was observed along with defoliation and dieback of oak stems, and massive mortality of herbs and sub-shrubs including *Dicerandra* (Menges, 2001).

Such reports prompted us to census a series of marked individuals of *Serenoa repens* (Bartr.) Small. (saw palmetto) and *Sabal etonia* Swingle ex Nash. (scrub palmetto), some of which have been monitored since January 1981, for drought impacts on palmetto survival and growth. Two hundred of the 940 marked palmettos in the study reported here as well as two seedling cohorts were burned in a February 2001 drought-related fire allowing us to observe the impacts of drought and intense fire on these flatwoods and scrubby flatwoods plants.

Specifically, we asked: (1) whether rates of mortality observed over the past two decades of monitoring changed for our marked adult or seedling palmettos in flatwoods, scrubby flatwoods, sand pine scrub, and southern ridge sandhill during the 2000–2001 drought, and (2) whether estimated total biomass changed during the drought period for the monitored adult palmettos and if heights changed for the monitored seedlings.

**METHODS**—Archbold Biological Station (ABS) is located near the southern terminus of the Florida peninsula's Lake Wales Ridge, 12 km south of the town of Lake Placid (27°11'N, 81°21'W). The

residual sandhills, relic beach ridges, and paleo-sand dunes (Brooks, 1981) create a rolling topography with elevations in the study area ranging from 38 to 61 m above mean sea level (U.S.G.S. Childs, Florida, 7.5' quadrangle). The lowest elevations commonly occupied by palmettos are in flatwoods on poorly drained to somewhat poorly drained soils, while the highest elevations inhabited by palmettos are in southern ridge sandhill vegetation on excessively well-drained sands. Between these extremes, palmettos occur in scrubby flatwoods, a transitional association between flatwoods and sand pine scrub, and, at slightly higher elevations relative to the water table, in sand pine scrub (Abrahamson, 1995; 1999).

Flatwoods range from low, open savanna-like associations dominated by *Serenoa repens*, *Aristida stricta*, and scattered *Pinus elliottii* var. *densa* or *P. palustris* to dense pine stands with thick shrub understories of *S. repens*, *Ilex glabra*, *Lyonia lucida*, and *Panicum abscissum*. The density and height of vegetation are dependent on edaphic conditions and time since last fire. Scrubby flatwoods are a low (1–2 m) shrubby association dominated by evergreen, xeromorphic oaks including *Quercus inopina*, *Q. chapmanii*, and *Q. geminata*, as well as abundant *S. repens* and *S. etonia*. The pines, *P. elliottii* var. *densa* and *P. clausa*, are typically widely scattered and occur at variable densities. A tree overstory of nearly even-aged *P. clausa*, an intermediate canopy of shrubby trees including *Carya floridana*, *Q. myrtifolia*, *Q. geminata*, and *Q. chapmanii*, and an understory of *Serenoa* and *Sabal* palmettos characterize sand pine scrub. Also a multilayered community, southern ridge sandhill has an overstory of *P. elliottii* var. *densa*, an intermediate deciduous canopy of *Q. laevis* and *C. floridana*, and a shrub and understory layer of *Q. myrtifolia*, *Q. geminata*, *Q. chapmanii*, *Serenoa*, *Sabal*, *A. stricta* and forbs. Details of these vegetative associations are available in Abrahamson and co-workers (1984), Abrahamson and Hartnett (1990), Myers (1990), Abrahamson and Abrahamson (1996a, b), and Menges (1999).

The climate of the study area is characterized by hot, wet summers and mild, dry winters. The highest monthly mean temperature (27.5°C) occurs in August and the lowest (16°C) in January. The rainy season normally extends from June through September, with an average of 60% of the annual precipitation (135.1 cm) falling during this 4-month period (Abrahamson et al., 1984; for regional climate information, see Chen and Gerber, 1990).

A total of 178 seedling palmettos were permanently marked in January 1989 to follow survival and growth rates in two populations, one in flatwoods ( $n = 100$ ) and another in scrubby flatwoods ( $n = 78$ ). Both sites were unburned since September 1984 until a February 2001 wildfire swept through both populations at the height of the drought. Each January through 1997 and again in October 2001, all seedlings were located and plants were measured for crown height and maximum crown width. Seedling palmettos were defined as small plants with grass-blade-like leaves (initially heights for all seedlings ranged from 1 to 25 cm with a mean of  $8.3 \pm 0.3$  cm [ $\pm$  standard error]). Excavations of similar plants in the vicinity of the monitored plants indicated that such plants were of seed origin and were not of sprout origin from rhizomes. These seedlings could not be identified to species as all individuals have only grass-blade-like leaves. The populations are likely a mix of both species given the occurrence of adults of both species around the seedlings.

A total of 940 permanently marked adult palmettos (469 *Serenoa* and 471 *Sabal*), representing a wide range of sizes, have been monitored at ABS for periods ranging from 11 years to 21 years in flatwoods (3 sites), scrubby flatwoods (3 sites), sand pine scrub (3 sites), and southern ridge sandhills (2 sites, Table 1). Censuses of all palmettos were conducted annually during January through 1997 and were measured again in October 2001. No measurements were made during January of 1998, 1999, 2000, or 2001. At each census, adult-sized palmettos (heights of all adult palmettos ranged from 27 to 196 cm during the period of 1989–1997) were measured or counted for crown height, crown maximum width, crown width perpendicular to the maximum width (referred to as crown “minimum”), number of living (i.e., green) leaves, number of leaves added since the last census (the most recent leaf is banded with a plastic-coated copper wire at each census), number of inflorescences (i.e., reproductive scapes) produced during the previous growing season, and the number of stem sprouts for *Serenoa*. All adult palmettos had fan-shaped leaves, which made identification of *Serenoa* and *Sabal* straightforward.

The fire histories of study sites vary with the most recent fire beginning on 12 February 2001 at the height of the drought (Table 1). This fire, likely started by a passing freight train, burned

TABLE 1. Adult and seedling palmetto populations monitored, monitoring periods, sample sizes, and fire occurrences.

Vegetation Association	Study Site	Monitoring Period*	Sample Sizes	Fire Occurrences
Flatwoods	WSP1	1981-2001	<i>Serenoa</i> = 20, <i>Sabal</i> = 20	Sep 1984, Feb 2001
	WS30	1981-2001	<i>Serenoa</i> = 20, <i>Sabal</i> = 20	Jan 1980, Mar 1990, Jun 1995
	Ridge Road	1981-2001	<i>Serenoa</i> = 20, <i>Sabal</i> = 20	Jul 1980, May 1989, Feb 2001
Scrubby Flatwoods	WSP2	1981-2001	<i>Serenoa</i> = 20, <i>Sabal</i> = 20	Sep 1984, Feb 2001
	Copse Road	1981-2001	<i>Serenoa</i> = 20, <i>Sabal</i> = 20	Jan 1980, Feb 2001
	Ridge Road	1981-2001	<i>Serenoa</i> = 20, <i>Sabal</i> = 20	Jul 1980, May 1989, Feb 2001
Sand Pine Scrub I	Burn	1985-2001	<i>Serenoa</i> = 50, <i>Sabal</i> = 50	Feb 1986
	Control	1985-2001	<i>Serenoa</i> = 49, <i>Sabal</i> = 51	1926 or 1927
	Control	1991-2001	<i>Serenoa</i> = 150, <i>Sabal</i> = 150	1926 or 1927
Sand Pine Scrub II	Burn	1989-2001	<i>Serenoa</i> = 50, <i>Sabal</i> = 50	Feb 1989, May 1991, May 1995
	Control	1989-2001	<i>Serenoa</i> = 50, <i>Sabal</i> = 50	1926 or 1927
	WSP1	1989-2001	Seedlings = 100	Sep 1984, Feb 2001
Flatwoods (seedlings)	WSP2	1989-2001	Seedlings = 78	Sep 1984, Feb 2001

\* Censuses were performed annually during January, however no censuses were performed in January of 1998, 1999, 2000, or 2001 and the 2001 census was conducted in October 2001.

approximately 259 ha making it the largest single fire on ABS property in 34 years of records. The high intensity of this wildfire and homogeneity of the burn were unprecedented at ABS (Menges, 2001). The severe drought along with several freezes that preceded this wildfire created very dry conditions that led the fire's unparalleled high intensity.

The total dry mass (aboveground and belowground) of each adult palmetto was estimated from regressions developed from 33 destructively harvested plants (17 *Serenoa* and 16 *Sabal*) of a wide range of adult sizes excavated from scrubby flatwoods and sand pine scrub (Abrahamson, 1995; 1999). These estimates provided non-destructive dry mass data for each palmetto at each census.

For *Serenoa*:

$$B = \text{Exp}(0.64 \ln C + 2.3 \ln L + 0.254)$$

$$r^2 = 0.84$$

For *Sabal*:

$$B = 10.71 C + 332.5 L - 826.3$$

$$r^2 = 0.86$$

where B = estimated dry mass (gm), C = crown "minimum" (cm), and L = number of living leaves.

SPSS Version 10.1 statistical software was used for all analyses (SPSS Inc., Chicago, IL) except for regression analyses, which were performed using *SigmaPlot 2001 for Windows* (SPSS Inc., Chicago, IL). Survival rates of seedlings and the changes in seedling heights over time were analyzed with first, second, and third-order regressions in order to find the best-fit model. Analysis of variance (ANOVA) was used to compare individual population means for seedling heights and the mass changes of adult palmettos by species and/or vegetation association, while a repeated-measures ANOVA was used to compare palmetto mass changes by species and vegetation association over time. When significant differences were found among three or more populations, Tukey post-hoc tests were used in conjunction with ANOVA to identify the specific populations that differed. Percentage changes in palmetto masses were arcsine-square root transformed prior to statistical analysis to improve normality.

**RESULTS—Drought and/or the February 2001 dry-season wildfire** appear to have caused substantial mortality to seedling palmettos in scrubby flatwoods, but had relatively little impact on seedlings in flatwoods (Fig. 1, top). After 8 years of monitoring (as of January 1997), cumulative survival of seedlings in the flatwoods cohort stood at 86% (14% mortality). Cumulative mortality in this cohort increased to only 30% (70% cumulative survival) in the subsequent nearly 5-year period (as of October 2001) suggesting that the drought and intense February 2001 wildfire had a relatively minor impact on seedling survival in flatwoods. In scrubby flatwoods, cumulative survivorship also stood at 86% in 1997 (14% mortality), but cumulative mortality more than tripled to 45% by October 2001 (55% cumulative survival).

Seedling heights have varied during the nearly 13-year monitoring period but have significantly increased in flatwoods over time while remaining unchanged in scrubby flatwoods. Mean heights of seedlings increased in flatwoods from 1997 ( $11.1 \pm 0.7$  cm) to 2001 ( $14.2 \pm 0.8$  cm) in part due to the death of smaller-sized seedlings (mean of dead seedlings was 9.8 cm) during the drought (Fig. 1, bottom). In contrast, the mean height of seedlings decreased in scrubby flatwoods from 1997 ( $9.4 \pm 0.7$  cm) to 2001 ( $7.9 \pm 0.6$  cm) where the mean of dead seedlings (7.3 cm) was not different than that of surviving seedlings. Maximum crown

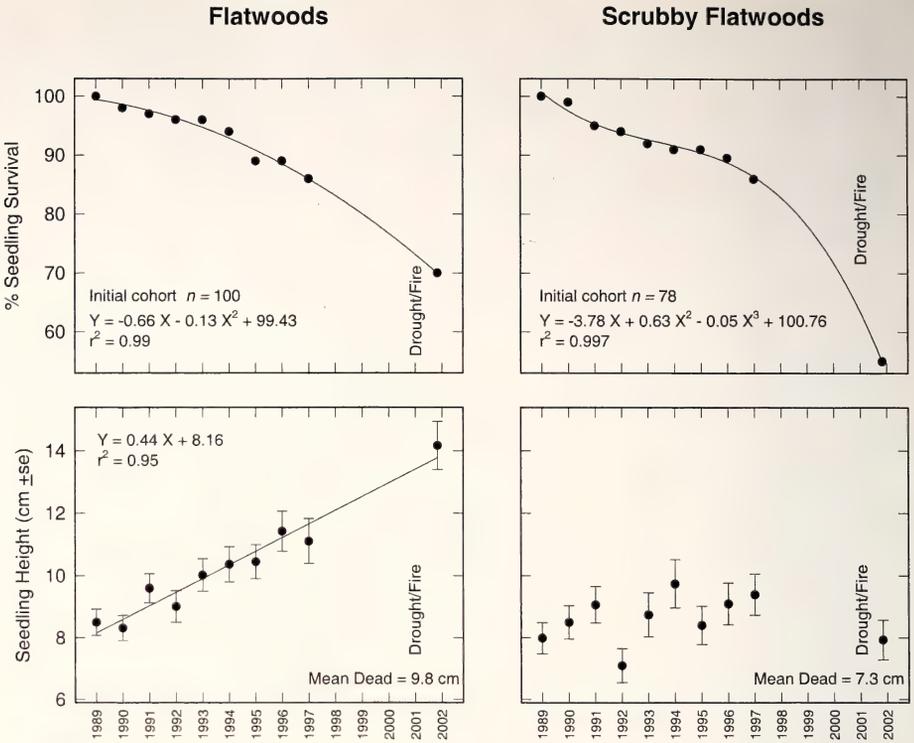


FIG. 1. The survivorship of seedling palmettos as a percentage of the original 1989 cohort and mean seedling heights  $\pm$  one standard error and over a nearly 13-year period (January 1989–October 2001) plotted against years. An intense dry-season wildfire swept through both the flatwoods and scrubby flatwoods study sites in February 2001 at the height of the 2000–2001 drought.

widths followed a similar pattern. Mean crowns for flatwoods seedlings in 1997 and 2001 were  $4.9 \pm 0.7$  cm and  $5.1 \pm 0.8$  cm, respectively while the same values for scrubby flatwoods seedlings were  $4.1 \pm 0.7$  cm and  $2.4 \pm 0.5$  cm, respectively. These results illustrate the slow transition of palmetto seedlings to adult, reproductive-sized individuals (also see Abrahamson, 1999).

Mortality of adult palmettos was minimal as only two deaths occurred between January 1997 and October 2001 (0.21% of the palmettos living in 1997). Both deaths occurred in much smaller-than-average individuals of *Sabal*. One in scrubby flatwoods had an estimated 1997 mass of 825 gm versus the mean of  $1310 \pm 72$  gm for scrubby flatwoods *Sabal*. This palmetto was burned in the February 2001 wildfire and failed to re-sprout. The other, with an estimated 1997 mass of 712 gm versus the mean of  $1625 \pm 77$  gm, was in southern ridge sandhill. With these two recent deaths, we have recorded a total of only five deaths (0.53% of the original 940 palmettos and only four of these five deaths were due to natural causes [0.43%]) during our two decades of monitoring. The death of one *Serenoa* in sand pine scrub had an anthropogenic origin caused by repeated

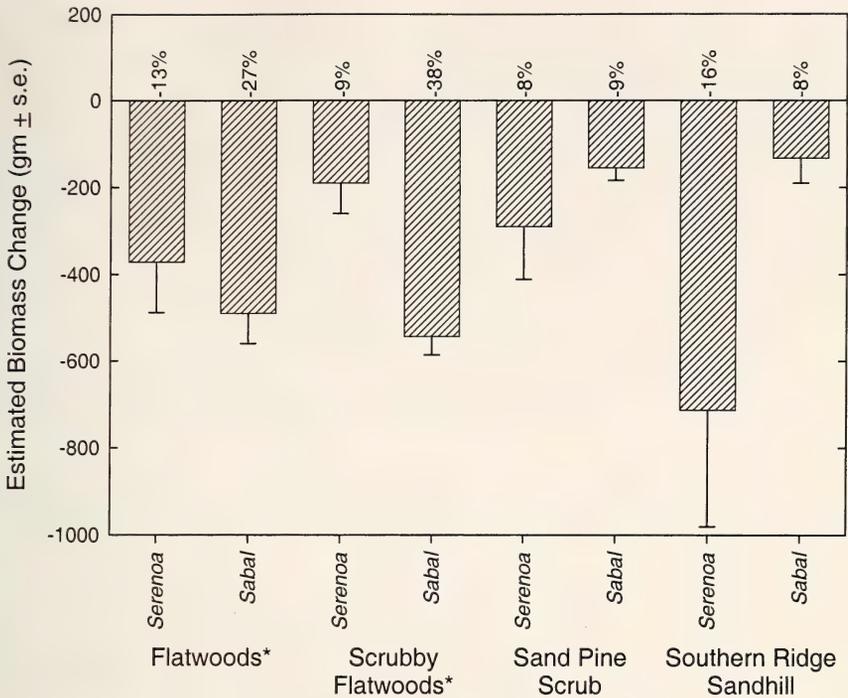


FIG. 2. Mean estimated changes in dry mass  $\pm$  standard errors for *Serenoa repens* and *Sabal etonia* in flatwoods ( $n = 60$  and  $60$  for *Serenoa* and *Sabal*, respectively), scrubby flatwoods ( $n = 60$  and  $60$ , respectively), sand pine scrub ( $n = 248$  and  $248$ , respectively), and southern ridge sandhill ( $n = 100$  and  $99$ , respectively). Biomass changes were calculated as the difference between the October 2001 estimated total dry mass (above and belowground) and the 5-year mean dry mass from 1993 to 1997, except for the southern ridge sandhill populations which were calculated as the difference between the October 2001 estimated dry mass and the January 1997 estimated dry mass because of a fire in May 1995. The percentage values associated with each bar indicate the percentage of change from the pre-drought mass. \*Two of the three flatwoods and all three of the scrubby flatwoods study sites were burned in the drought-related intense February 2001 wildfire.

chopping activities connected to trail maintenance. Two of the natural-origin deaths occurred to *Sabals* in sand pine scrub and included a small-sized individual (died in 1997) and a palmetto that was pried out of the ground when a nearby *Pinus clausa* tipped up (died in 1994). The remaining two natural-origin deaths are those recorded between January 1997 and October 2001 and are likely related to drought, and in one case the combined impacts of drought and fire. These extremely low rates of mortality suggest extraordinary longevities for both *S. repens* and *S. etonia*.

*Serenoa* and *Sabal*, on average, lost mass during the drought across all vegetative associations (Fig. 2). *Serenoa*'s mean pre-drought estimated mass was  $3492 \pm 152$  gm compared to a post-drought mean of  $3069 \pm 132$  gm ( $-12\%$  of the pre-drought mass,  $n = 468$ ). Similar values for *Sabal* were  $1645 \pm 31$  gm (pre-drought) and  $1416 \pm 32$  gm (post-drought,  $-14\%$ ,  $n = 466$ ). A repeated-measures

ANOVA showed that palmettos significantly lost mass between the pre-drought and post-drought censuses ( $F = 55.8, p < 0.001$ ) and that the 3-way interaction of census date  $\times$  palmetto species  $\times$  association was significant ( $F = 6.2, p < 0.001$ ). The two-way interaction terms were not significant. Furthermore, the between-subjects portion of this analysis indicated that *Serenoa* were significantly larger on average than *Sabal* ( $F_{1,926} = 97.4, p < 0.001$ ) and that palmettos growing in the various vegetation associations differed significantly in mass ( $F_{3,296} = 11.5, p < 0.001$ ). The between-subjects interaction of species  $\times$  association was also significant ( $F_{3,926} = 6.6, p < 0.001$ ) suggesting that the two palmetto species had differing patterns of mass (size) across vegetative associations. A Tukey post-hoc test indicated that palmettos in the more closed-canopied and better-drained southern ridge sandhill and sand pine scrub were significantly larger on average than palmettos in more open-canopied and less well-drained scrubby flatwoods and flatwoods.

Although all flatwoods and scrubby flatwoods *Serenoa* and *Sabal* populations lost mass during the drought, these losses were not due entirely to drought. Five of the six populations in these associations were burned in the intense February 2001 wildfire. Thus, the burned palmettos had only 8 months of recovery after fire at the time of our October 2001 census. Consequently, a comparison of mass losses for *Serenoa* and *Sabal* at the WS30 flatwoods site, the only flatwoods or scrubby flatwoods population not impacted by the February 2001 wildfire, against the losses at the five burned flatwoods and scrubby flatwoods found significant differences among the populations ( $F_{4,228} = 7.77, p < 0.001$ ). However, although unburned, WS30 palmettos showed mass losses, albeit the least loss among the flatwoods and scrubby flatwoods populations, with an average loss of  $-57$  gm during the drought. This loss for unburned palmettos was not significantly different from the losses at two burned scrubby flatwoods populations, which showed changes of  $-224$  gm and  $-373$  gm. Furthermore, the absolute and relative mass losses were greater for *Sabal* than for *Serenoa* ( $F_{1,236} = 9.8, p = 0.002$  and  $F_{1,234} = 34.7, p < 0.001$  for absolute and arcsine-square-root transformed percentage change, respectively; Fig. 2).

Because no fires occurred in any of the sand pine scrub populations after February 1986, these plants provide a more direct estimate of potential drought impacts on the growth performance of palmettos than do the flatwoods and scrubby flatwoods palmettos. Overall, *Serenoa* in the sand pine scrub populations had a post-drought mean mass that was  $290 \pm 121$  gm less ( $-8\%$ ) than the mean for the pre-drought mass (Fig. 2). *Sabal* in sand pine scrub lost somewhat less mass during the drought with a mean loss of  $155 \pm 29$  gm ( $-9\%$ ).

One of the two southern ridge sandhill populations experienced fires in February 1989, May 1991, and May 1995; the other population has been unburned since 1926 or 1927. Consequently we contrasted only the January 1997 estimated mass with that of October 2001 to ensure full mass recovery by burned palmettos (Abrahamson, 1995; 1999). The southern ridge sandhill *Serenoa* lost  $713 \pm 268$  gm during the drought (the largest absolute mass loss recorded,  $-16\%$ ), while *Sabal* lost  $133 \pm 57$  gm ( $-11\%$ , Fig. 2).

TABLE 2. The percentages of adult palmettos that lost mass and percentages of seedlings that lost height during the drought period.

Vegetation Association	Study Site	Percentage of palmettos losing mass (adults) or height (seedlings)	
		<i>Serenoa repens</i>	<i>Sabal etonia</i>
Flatwoods	WSP1*	70	100
	WS30	65	60
	Ridge Road*	90	95
Scrubby Flatwoods	WSP2*	95	100
	Copse Road*	50	100
	Ridge Road*	80	100
Sand Pine Scrub I	Burn + Control	66	66
Sand Pine Scrub II		53	59
Southern Ridge Sandhill	Burn + Control	61	55
Flatwoods (seedlings)	WSP1		19
Scrubby Flatwoods (seedlings)	WSP2		63

\* Sites burned in the February 2001 wildfire.

An examination of mass changes during the drought by individual palmettos found that the majority of adult palmettos at each study site lost mass, however the percentage of palmettos losing mass varied by species, vegetative association, and whether burned in the February 2001 wildfire (Table 2). For example, burned *Sabal* tended to have a higher percentage of individuals that lost mass than did burned *Serenoa*. Furthermore, the percentage of individual palmettos that lost mass was higher in the burned flatwoods than in the unburned flatwoods. This difference is likely due to the relatively short 8-month recovery period rather than the drought. The percentages of individual palmettos losing mass in sand pine scrub and southern ridge sandhills was comparable to the percentages seen at the unburned flatwoods.

The percentage of surviving palmetto seedlings that lost height varied markedly between flatwoods and scrubby flatwoods (Table 2). Similar to the pattern of higher mortality among seedlings in scrubby flatwoods compared to flatwoods seedlings, 63% of the seedlings in the scrubby flatwoods cohort lost height while only 19% of the flatwoods seedlings lost height.

DISCUSSION—Overall, the severe drought that began its grip on the Florida peninsula in April 1998 and persisted until March 2001 had relatively little impact on *Serenoa repens* and *Sabal etonia*. Adult survival through the drought was high, even when an intense wildfire swept through palmettos at the height of the drought. We recorded mortality to only two smaller-than-the-average adult *Sabals* out of the 937 palmettos alive prior to the drought. All but one (0.5%) of the 200 adult palmettos that were intensely burned in February 2001 survived. Although both species are well adapted to survive fire given their extensive underground resources, both palmettos evolved under a regime of wet-season rather than dry-season fires (Abrahamson, 1984; 1995). Thus, our finding that an intense

dry-season fire that occurred during a severe and prolonged drought had little impact on survival illustrates the extraordinary persistence of these palmetto species.

Palmetto mass declined in all monitored populations from pre-drought to the post-drought censuses. However, the degree of change in both the absolute and relative mass varied by individual palmetto, species, and from population to population. For example, the only populations in which all individuals lost mass were those that were burned. The percentages of unburned individuals that lost mass at the different sites varied from 53 to 66%, illustrating that a large portion of palmettos survived the drought with gains, rather than losses, in mass. The two palmetto species also differed. The smaller *Sabal* palmettos were more affected than the larger *Serenoa* in flatwoods and scrubby flatwoods for losses in both absolute and relative mass. However, *Serenoa* were more impacted in absolute mass in sand pine scrub and southern ridge sandhill compared to *Sabal*. This pattern of impact fits well with the greater dominance of *Serenoa* in flatwoods and scrubby flatwoods and of *Sabal* in sand pine scrub and southern ridge sandhills (Abrahamson, 1995).

The greatest drought impact was on palmetto seedling survival, however even here enhanced mortality was observed in only one of the two seedling cohorts. The survival of the majority of seedlings in both flatwoods and scrubby flatwoods was impressive given the consumption by fire of their aboveground parts at the height of the drought, and the persistence and intensity of the drought. Some 70% of the original flatwoods cohort and 55% of the original scrubby flatwoods cohort survived through nearly 13 years, a severe and prolonged drought, and an intense wildfire. The higher survival of flatwoods seedlings indicates that drought and/or the intense February 2001 wildfire more adversely affected seedling survival in scrubby flatwoods. Scrubby flatwoods occur on better-drained soils than do flatwoods, which may have enhanced the impacts of drought and/or lessened the ability to recover following fire.

Although we believe that our results are intriguing and the conclusions are robust, there are several limitations in our study. First, we don't know if all of the demographic effects of the drought on palmettos are complete. It is possible that additional mortality could occur at some future time that is at least indirectly related to the impacts of the 2000–2001 drought. Second, is the drought really over? Although precipitation levels were near normal during the summer of 2001, the winter of 2001–2002 was not particularly wet. Finally, although our regression equations to estimate total aboveground and belowground mass were developed from palmettos harvested during the dry season, these equations may not adequately represent losses that occur during drought. For example, if our palmettos primarily lost mass aboveground (the portions of the plants that we measured) during the drought and lost little if any mass belowground, we have overestimated the impacts of drought on plant mass. If so, then the take-home message of this study, that *Serenoa* and *Sabal* show extraordinary persistence and tolerance to severe drought and intense dry-season wildfire, would become even stronger.

Previous studies (Hilmon, 1969; Abrahamson, 1984; 1995; 1999) have illustrated the longevity, persistence, and resilience after fire of *Serenoa repens* and

*Sabal etonia*. The results presented here demonstrate the ability of these palmettos to persist through severe and prolonged drought as well as intense wildfire even when it occurs during the dry season at the height of a drought. These two palmetto species are well adapted to the rigors (i.e., winter dry seasons, nutrient-poor soils) of Florida's xeric uplands and to the variability of the Florida peninsula's climate. However, they are now also exposed to a human-altered fire regime that includes dry-season fire. Upland Florida plants such as these palmettos evolved with wet-season fire but likely experienced dry-season fires rarely during their evolution (Abrahamson et al., 1984; Abrahamson and Hartnett, 1990; Myers, 1990). The persistence of these two species is threatened primarily by anthropogenic factors rather than by natural phenomena (Peroni and Abrahamson, 1985; Abrahamson, 1995; 1999; Benschhoff, 1995).

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## REVIEW

Walter E. Meshaka, Jr. *The Cuban Treefrog in Florida. Life History of a Successful Colonizing Species*, University of Florida Press, Gainesville, FL. 2001. pp xxiii + 191. Price: \$69.95, clothbound.

THE Cuban treefrog is one of the most successful vertebrate colonists in southern Florida, an area replete with invasive species. Reported from the lower Florida Keys in the early 1930s, the Cuban treefrog now occurs throughout the Keys and the southern half of the Florida peninsula. Its large size allows it to consume a wide variety of invertebrate and vertebrate prey, including native species of frogs. It may thus be a serious predator on and/or a competitor with, native frogs. Yet few details are known of the life history of this extraordinary colonist, and little of substance is known concerning the impact of this invasive species on native Florida frogs. Thus, Walter Meshaka's book on the Cuban treefrog in Florida—based largely on his doctoral dissertation—is potentially important in documenting the life history of this species in southern Florida and in detailing the effects of this Caribbean interloper on native species.

The treatment includes consideration of the geographic distribution of the Cuban treefrog, its relationship to other members of its genus, and the history of its colonization of Florida. The environment of southern Florida is described with special reference to the Everglades, and a brief chapter outlines the author's methods and the organization of the study. The bulk of the book documents reproduction, larval development and post-metamorphic growth, behavior, habitat selection, stomach contents and diet overlap with potentially competing species, predation, and sexual size dimorphism. The book includes a one and a half page conjecture on the possibility of future geographic expansion of the Cuban treefrog into other parts of the United States and in the Caribbean, and it concludes with an equally brief chapter on the future of the Cuban treefrog in the Everglades.

Clearly much work was involved in compiling the information that forms the basis of this book. Unfortunately, the same cannot be said for the preparation of the manuscript, which appears to have received little or no copy editing. The result is a text with numerous run-on sentences, incomplete sentences, awkward constructions, and pronouns with ambiguous antecedents. In the aggregate these deficiencies often obscure the author's meaning.

The book appears to have suffered from want of rigorous peer review. A section entitled "larval growth" for example, actually deals with the duration of the larval period and size at metamorphosis. Statistical conventions are frequently violated. For example, probabilities are sometimes symbolized as upper case "P," other times as lower case. F-ratios are reported variously and inconsistently to two, three, or four decimal places. In Figure 1, time is plotted on the Y-axis. Many bivariate plots showing non-significant regressions are illustrated, complete with regression equations and coefficients of determination; considerable space could have been saved by excluding these uninformative graphs and simply reporting the relevant

statistics in the text. Several regressions reported as statistically significant are of doubtful biological significance because statistical assumptions are violated, or because a few outlying data points have disproportionately large leverage. Some tables are poorly set and are confusing, and in some the standard deviations are indicated with  $\pm$ , but with only a + in others.

Of the 33 black and white photographs of habitat, several appear underexposed and/or out of focus in my review copy. Many graphs are poorly designed. Some have different font sizes within a single graph. Some graphs include regression equations, others do not. Apparently there were problems in formatting the graphs, for some have broken regression lines, others have peculiar symbols and lines appearing on them without explanation. The axis labels are miss-set on some graphs, and others have labels that overlap, and thus obscure, data points. The book is organized in logical fashion, but two chapters consist of only one and a half pages each and several others do not exceed five pages. These could have been integrated with other chapters or combined to better affect. The book is over-illustrated, with unnecessary graphs, and tables that contain material duplicated elsewhere. In the scant space of 191 pages, there are 142 figures and tables, an average of one figure or table for every 1.3 pages.

*The Cuban Treefrog* is a data rich volume, the result of the author's energetic and enthusiastic pursuit of his study of this species. He has succeeded in amassing a large volume of information on this important invasive species, and he is unquestionably the foremost authority on its biology. Sadly, the deficiencies in editing, peer review, and production seriously detract from the usefulness of this slim, overpriced volume.—Julian C. Lee, Department of Biology, University of Miami, Coral Gables, [jlee@bio.miami.edu](mailto:jlee@bio.miami.edu).

# FLORIDA SCIENTIST

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